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The Late Cretaceous Environment of the Arctic: A Quantitative Reassessment based on Plant Fossils

Robert A. Spicer^a and Alexei B. Herman^b

^aDepartment of Earth and Environmental Sciences, Centre for Earth,
Planetary, Space and Astronomical Sciences, The Open University, Milton
Keynes, MK7 6AA, UK.

^b Geological Institute, Russian Academy of Sciences, 7 Pyzhevskii Per.,
119017 Moscow, Russia.

r.a.spicer@open.ac.uk

Abstract

Late Cretaceous megafossil floras from the palaeo-Arctic of northeastern Russia and northern Alaska are reviewed in respect of their age, composition, structure and floral dynamics. Palaeofloral correlations and comparisons are made between the two regions. Nine angiosperm-rich, predominantly Cenomanian to Coniacian, floras from the palaeo-Arctic are re-evaluated using Climate Leaf Analysis Multivariate Program (CLAMP) calibrated using a global gridded (0.5° x 0.5°) climate data set derived from that used in climate modelling. Additional floras from lower palaeolatitudes were used to derive latitudinal temperature gradients: seven from N. America, five from around 30°N palaeolatitude in Europe and one from Kazakhstan. The Arctic climatic

determinations, similar to previous estimates, support the existence of a northern Pacific Ocean cold gyre and a warm Arctic Ocean. At palaeolatitudes greater than 80°N floras are insufficiently diverse in woody dicot taxa to use CLAMP, but using CLAMP-derived latitudinal temperature gradients Arctic Ocean coastal environments at 70 Ma and 82°N, and which supported a diverse dinosaur megafauna, are predicted to have experienced a mean annual temperature of $6.3 \pm 2.2^{\circ}\text{C}$, a warm month mean of $14.5 \pm 3.1^{\circ}\text{C}$ and a cold month mean no colder than $-2.0 \pm 3.9^{\circ}\text{C}$. All uncertainties are 2σ . The new estimates are in good agreement with a wide range of non-palaeobotanical climate proxies and render as an outlier warmer temperature estimates for the Arctic Ocean derived from the TEX_{86} proxy. Modelling, however, shows that land to ocean temperature gradients could have been steep. The CLAMP estimates also suggest high values for humidity and precipitation consistent with sedimentological indicators and, coupled with warm temperatures, support the existence of a persistent polar cloud cap that helped maintain high terrestrial air temperatures throughout prolonged periods (up to 5 months) of winter darkness.

Keywords: Late Cretaceous; Arctic; climate; vegetation; CLAMP; plant fossils

1. Introduction

The existence of fossil floras attesting to vigorous forest growth in polar regions (palaeolatitudes $> 66^{\circ}$) during Mesozoic and early Tertiary times has

51 been long been used as evidence for significant natural global climate
52 change. In 1914 the palaeobotanist Marie Stopes underscored the importance
53 of polar floras in a climatic context by quoting Asa Gray as saying "Fossil
54 plants are the thermometers of the ages by which climatic extremes and
55 climate in general through long periods are best measured" and cites Darwin
56 who, in a letter to Hooker in 1881, wrote "The extreme importance of the
57 Arctic fossil plants is self evident", and went on to urge Hooker to "Take the
58 opportunity of groaning over our ignorance of the lignite plants of Kerguelen
59 Land or any Antarctic land. It might do good." (Stopes, 1914).

60 Since then our understanding of plate tectonics has emphasized the
61 extent of climate change by showing that in most cases these ancient polar
62 plants were growing at even higher palaeolatitudes than originally thought
63 when continents were regarded as fixed. In the Arctic abundant leaf fossils, in
64 situ trees and dinosaur remains are preserved from sites that were at the
65 highest known palaeolatitudes where land existed (Brouwers et al., 1987;
66 Clemens, 1994; Clemens and Nelms, 1993; Fiorillo, 2008; Fiorillo and
67 Gangloff, 2000; Fiorillo et al., 2009; Gangloff, 1998; Gangloff et al., 2005;
68 Spicer and Parrish, 1987; Spicer and Parrish, 1990b) and in some
69 reconstructions close to the North Pole itself (Fig. 1). That said, the tectonics
70 of the Arctic are complex and differences in plate reconstructions result in
71 differences in the palaeo-positions of individual fossils sites. For example
72 Figure 1 shows north polar projections for 100 Ma, 88 Ma and 70 Ma derived
73 data compiled by Hay et al. (1999). Important differences exist between these
74 reconstructions and others in widespread use (e.g. Smith et al., 1981; Ziegler
75 et al., 1983). Uncertainties for Alaskan Campanian-Maastrichtian

76 palaeolatitudes have been quoted as +4 to −9° (Amniot et al., 2004). Unless
77 otherwise indicated the palaeolatitudes quoted here are those provided in
78 original publications that in some cases are based on palaeomagnetic data
79 local to the fossil sites. However, those locations should be considered
80 against those suggested in Figure 1 as an indication of the uncertainties
81 involved. For internal consistency the calculation of equator-to-pole
82 temperature gradients presented later in this paper use the plate positioning
83 programme Point Tracker (Scotese, per comm. to RAS, 2009).

84
85 [Figure 1 near here]

86
87 During the greenhouse climates of the Mesozoic zones of maximum
88 non-marine organic productivity, as evidenced by the mapping of fossil
89 remains and climatically sensitive sediments, were significantly polewards of
90 the equator (Chumakov et al., 1995; Rees et al., 2000; Semikhatov and
91 Chumakov, 2004; Spicer, 2003). In the Arctic widespread Late Cretaceous
92 sediments across Alaska, Canada and Russia contain an exceptionally rich
93 fossil record that provides a window into a time of abundant primary
94 productivity, carbon sequestration, and insights into a climatic regime that
95 provide a potential blueprint for managing future Arctic environmental change.

96 The areas of the Arctic where the most detailed and extensive
97 palaeobotanical and sedimentological records exist at the highest
98 palaeolatitudes are in northeastern Russia, Siberia and Northern Alaska and
99 they form the basis of this review and re-evaluation (Fig. 2). Comparable sites
100 representing such high palaeolatitudes are not currently accessible in the

Southern Hemisphere, so the Arctic provides our only insight into truly polar conditions during the Late Cretaceous. In this paper previous palaeoclimate estimates using these floras are reviewed and revised using a new recalibration (Spicer et al., 2009a) of the multivariate foliar physiognomic technique known as CLAMP (Climate Leaf Analysis Multivariate Program) based on the global 0.5° x 0.5° gridded meteorological data of New et al. (1999).

[Figure 2 near here]

2. Cretaceous Floras from Alaska

In northern Alaska Late Cretaceous active deltaic sedimentation bequeathed an unparalleled legacy of inter-fingering marine and non-marine fossiliferous sediments that allow high-resolution reconstructions of this warm polar regime for which there is no modern analogue. Sediment shedding from the south into the Colville Basin led to the development, throughout the Late Cretaceous, of alluvial coastal plains incorporating the river-dominated Corwin and Umiat Delta complexes (Huffman et al., 1985; Huffman, 1985). In the west progradation was predominantly north and eastwards, while in the east the coastal plain extended northwards forming what would later become the central Arctic Slope of Alaska. The various marine and non-marine sediments were originally divided into the Nanushuk and Colville Groups. The geology of the Nanushuk Group is discussed in detail in Ahlbrandt (1979) and Huffman (1985), while that of the Colville is presented in Brosgé and Whittington,

(1966) and Molenaar et al. (1987). Mull et al. (2003) revised the stratigraphic nomenclature of the Arctic Slope and it is their scheme (Fig. 3) that is followed here. For ease of referring to the older literature now abandoned nomenclature is also used, but enclosed in square brackets. This convention is incorporated in Figures 4, 5 and 7 that summarize the floral occurrences and relationships. Late Cretaceous Arctic Slope sediments, as well as those across N.E. Russia, consist of intertonguing marine and non-marine units allowing for a rigorous biostratigraphic framework correlating both marine and non-marine realms. In addition, abundant bentonites in the Late Cretaceous have yielded some radiometric constraints (e.g. Bergman et al., 2006; Conrad et al. 1992; Lanphere and Tailleux, 1983).

[Figure 3 near here]

The alluvial plain sediments of northern Alaska yield exceptionally rich plant megafossil assemblages ranging in age from Albian (possibly Aptian) through to Maastrichtian (Scott and Smiley, 1979; Smiley, 1966; Smiley, 1967; Smiley, 1969a; Smiley, 1969b; Spicer, 1983; Spicer and Parrish, 1986; Spicer, 2003; Spicer and Herman, 2001), the only major hiatus being the result of a regional late Cenomanian/early Turonian transgression. These non-marine Cretaceous successions also contain more than 2.7×10^{12} tonnes of low sulphur, low ash coal (Sable and Stricker, 1987); reportedly one third of all US coal reserves of all ages combined. By studying the assemblages in a sedimentary facies context, the vegetational communities have been reconstructed in detail and allowed the first quantitative estimates to be made

of Cretaceous near-polar air temperatures and precipitation (Spicer and Parrish, 1986; Spicer, 1987; Parrish and Spicer, 1988a; Spicer and Parrish, 1990a).

Palaeosols are abundant in the Late Cretaceous successions of northern Alaska and are characterised by gleyed colours, rare root traces but abundant organic matter, abundant siderite, rare clay and silty clay coatings and infillings, some preservation of sedimentary stratification and a general lack of ferruginous oxides and mottles. They are interpreted as being poorly drained, reducing, hydromorphic soils similar to modern Inceptisols (Ufnar et al., 2004).

In the 1960s C. J. Smiley collected plant material from the central and western North Slope of Alaska. However, although these and other collections made by him formed the basis of a regional phyt stratigraphic scheme (Smiley, 1966; Smiley, 1967; Smiley, 1969a; Smiley, 1969b), the floras were never formally described, illustrated, or even listed. The only exception is a summary paper by Scott and Smiley (1979). Moreover, Smiley was not able to compare his material directly to that from North-eastern Russia and Russian workers only had the names of some typical taxa reported by Smiley as their Alaskan reference material. Now at the Smithsonian Institution National Museum of Natural History, Smiley's collections have been studied and photographed by us in the context of museum collections held in Russia and our own extensive collections from both Alaska and N.E. Russia. In due course all of this material, currently amounting to over 10,000 images, will be made available on-line.

Based on a combination of Smiley's material, subsequent collections from Alaska, and comparisons with Russian collections, Albian vegetation in northern Alaska appears typically to have been dominated by deciduous conifers such as *Cephalotaxopsis*, *Podozamites*, and *Pityophyllum* with deciduous ginkgophytes (*Ginkgo* and *Sphenobaiera*) forming thickets along river margins and in mires (Spicer and Herman, 2001). Ferns and *Equisetites* were the main herbs with deciduous vine-like cycads, (quite unlike their modern evergreen thermophilic relatives) occurring locally (Herman and Spicer, 1996a).

This combination of Alaskan and N.E. Russian plant fossil assemblages (taphofloras) has also allowed the development of phyt stratigraphic correlations throughout the North Pacific region. Herman (2007a, b, c) described a number of regional phyt stratigraphic units; each unit was defined as plant-bearing deposits containing fossil floras of a certain type characterised by their taxonomic composition determined by both evolution and environment (and therefore representing a certain phase of regional floral evolution). Each of these floral units, here termed a "regional palaeoflora", is typified by a reference taphoflora, which is one of several taphofloras with essentially similar characteristics that belong to that regional palaeoflora. Within a given geographic range a regional palaeoflora has a correlative function across formations and their subdivisions, while a palaeofloral 'stage' reflects a phase of evolutionary development. For an extended discussion of these concepts see Herman (2007a).

This approach is exemplified by taphofloras recovered from 34 localities representing alluvial floodplain environments along the Kukpowruk River,

western North Slope Alaska (Spicer and Herman, 2001), that serve as the type flora of the Kukpowruk floral stage and the Kukpowruk regional palaeoflora. Other taphofloras that are assigned to the same floral stage are the Kokolik, the Corwin Bluff, Pitmegea River, Punak Creek, taphofloras from members 1–4 of the Kuk-Kaolak section, and by the Lower Killik taphoflora from the Umiat-Chandler area (Fig. 4). Taken together these taphofloras point to the Kukpowruk floral stage being taxonomically diverse with over 100 taxa (Spicer and Herman, 2001; Herman and Spicer, 2002) including liverworts (?), sphenophytes, ferns, cycadophytes, czekanowskialeans, caytonialeans (?), conifers, gymnosperms of unknown affinity, angiosperms and remains that so far elude identification.

[Figure 4 near here].

The lower boundary of the Kukpowruk floral stage in the Umiat-Chandler area of the Arctic Slope directly overlies the marine beds of the Nanushuk Formation [Tuktu Formation] containing *Gastrolites*, *Cleonicerias*, *Inoceramus anglicus* Woods and *I. Cadottensis* McLearn (Detterman et al., 1963, Smiley, 1969a), which indicate a basal middle Albian age. In the Kuk-Kaolak area *Entolium* sp. in the upper part of Smiley's (1966) Lithological Unit 1 (Fig. 4) underlies the plant-bearing beds and suggests an age no older than middle Albian (Imlay, 1961, cited in Smiley, 1966). Further to the west in the Utukok-Corwin region the middle Albian *Paragastrolites spiekeri* McLearn is found in the upper part of the Lower Nanushuk Formation [Kukpowruk

Formation] (Chapman and Sable, 1960). Thus the Kukpowruk floral stage is likely to have begun in middle Albian time.

The upper age limit of the Kukpowruk floral stage is in the uppermost part of the Albian because regionally rocks containing the floral stage are conformably overlain by deposits containing taphofloras of the Niakogan floral stage, which in turn is correlative with the Albian – Cenomanian Grebenka flora of the Anadyr-Koryak subregion. The Grebenka flora is well dated by both marine biostratigraphic and isotopic ($^{40}\text{Ar}/^{39}\text{Ar}$) methods (Spicer et al. 2002). Herman (2007b) estimated the duration of the Kukpowruk floral stage to be 8-9 m.y.. The ages and duration of other Alaskan and N.E. Russian floral stages and horizons are similarly constrained and the correlations are summarised in Figures 4-7.

Detailed recording of repeated plant associations in sedimentary context has not only provided the basis for phyt stratigraphic correlation, but also an understanding of ancient plant community succession. For the Kukpowruk flora this typically began with *Equisetites* colonising bare river bank substrate surfaces, quickly joined by the fern *Birisia* which often formed expansive *Birisia* marsh 'heaths' in low-lying interfluvial areas. As seral development continued *Arctopteris* (a fern) and the cycadophyte *Nilssonina* typically would then dominate leaving *Equisetites* and *Birisia* as subordinate elements. River margins were usually dominated by ginkgophytes, but in mire environments stable state communities culminated in a *Podozamites* and *Pityophyllum*-dominated shrub 'woodland' with *Birisia* and *Equisetites* remaining as the main understorey components. In drier settings a more diverse community developed, again dominated by the conifer-like

249 *Podozamites* and *Pityophyllum*, but with *Desmiophyllum* and sometimes
250 *Arctopteris* as typical subordinate elements joining *Birisia* and *Equisetites*
251 (Spicer and Herman, 2001)

252 Overall the Kukpowruk and co-eval taphofloras in northern Alaska (Fig.
253 4) show high levels of similarity with the Buor-Kemyus regional palaeoflora in
254 N.E. Russia (Figs. 5 and 7).

255

256 [Figure 5 near here]

257

258 Flowering plants migrated into Northern Alaska in the late Albian from lower
259 latitudes (Scott and Smiley, 1979; Spicer and Parrish, 1986; Spicer, 1987)
260 and began to oust the ginkgophytes from their riparian habitats. Typical of the
261 earliest angiosperms to appear in northern Alaska are those found in the
262 youngest (latest Albian to early Cenomanian Nanushuk Formation [Corwin
263 Fm.]) of the Kukpowruk River assemblages (Spicer and Herman, 2001). As in
264 Russia, the migration pathways of these opportunists appear to have been
265 along coastal margins and along disturbed river habitats (Herman, 2002). In
266 Alaska this is evident both from channel sands in the Nanushuk Formation
267 (later Kukpowruk and Niakogon regional palaeofloras in Fig. 4), as well as in
268 the Cenomanian and Turonian fluvial deposits of the Yukon-Koyukuk Basin
269 (Hollick, 1930; Spicer, 1983). Platanoid (sycamore)-like leaves are the most
270 abundant angiosperm megafossils in channel sands, crevasse splay and
271 overbank settings in latest Albian through the Cenomanian. As the Late
272 Cretaceous progressed evolutionary novelty, combined with a low competitive
273 stress from the non-angiosperms, polyploidy and hybridization (Spicer, 1986)

led to a diversity of flowering plant leaf forms occupying the full range of alluvial floodplain environments except mires. However, diversity at the family level was low and no major clades (families or higher taxonomic ranks) appear to have originated in the high Arctic (Spicer et al., 1987; *contra* Hickey et al., 1983).

Fossil trees, many in growth position and up to 70 cm in diameter, are abundant in Nanushuk [Niakogon Tongue] non-marine rocks and cell details are often preserved (Spicer, 2003). Productivity evidently was high and tree ring characteristics show that intra-annual environmental variation was small. Seasonality, however, was extreme and typically the rings exhibit sudden transitions from earlywood to latewood indicating a short autumnal period, and small quantities of latewood suggest deep dormancy. Here, as in previous studies of Alaskan North Slope woods (Parrish and Spicer, 1988b; Spicer and Parrish, 1990a), latewood is differentiated from earlywood using the classical definition of these terms as originally proposed by Mork (1928) and clarified by Denne (1989). The concept of earlywood used by Creber and Chaloner (1984) and Falcon-lang (2005) has been criticized in the context of characterizing high latitude light regimes (Taylor and Ryberg, 2007) and is not used here. Evidently the transition from full summer growth to winter dormancy was rapid (< 3 weeks), consistent with a high palaeolatitude and obliquity angle essentially similar to that of the present (Parrish and Spicer, 1988b).

Palaeogeographic reconstructions (Smith et al., 1981; Ziegler et al., 1983), and palaeomagnetic data from the Nanushuk Formation itself (Witte et al., 1987) indicate the area was at least 75 °N during the Cenomanian

although some reconstructions place it closer to the pole (Hay et al., 1999; <http://www.odsn.de/>)(Fig.1). A relative northward drift of Northern Alaska through the Late Cretaceous positioned the Maastrichtian northern coastline of Alaska at approximately 85 °N (Smith et al., 1981; Ziegler et al., 1983). Best fit distribution of coals and other climatically sensitive sediments show that the rotational pole was within 4° of the palaeomagnetic pole in the Maastrichtian (Lottes, 1987). Thus throughout the Late Cretaceous the Northern Alaska winter, assuming a minimum palaeolatitude of 71 °N to a maximum of 89 °N, was characterised by between almost 2 months of continuous twilight to almost 5 months of continuous darkness bounded by a total of three months of bounding twilight (Anonymous, 1978)(Fig. 8). This extended period of darkness is consistent with the small latewood components of the tree rings and rapid transitions from earlywood to latewood cell formation.

Wood anatomy (Parrish and Spicer, 1988b), vegetation composition and angiosperm (dicot) leaf margin analysis indicates that the Cenomanian mean annual air temperature on the coastal plain was approximately 10 °C. The mean annual range of temperature could have been over 20 °C, but cold month means were no lower than -11 °C (Spicer and Parrish, 1986; Parrish et al., 1987; Spicer and Parrish, 1990a) and could well have been warmer. Large ranges of leaf size, coupled with lack of thick cuticles and lack of damage to wood cells, suggests evapo-transpirational stress was low at all times during the growing season, including the early spring. Coupled with sedimentological data indicating a lack of periglacial features, this indicates that freezing of the root zones did not occur to any extent.

324 Precipitation was high as evidenced by exceptional quantities of coal
325 accumulation. Contrary to early USGS reports, pollen preservation in the
326 coals and associated clastic facies can be good (Youtcheff et al., 1987) and
327 preparations have yielded significant pollen stratigraphic changes on the
328 millimetre scale within coals (Grant et al., 1988). Many mires, particularly in
329 the Campanian and Maastrichtian, were undoubtedly low lying and
330 maintained by a high regional water table. In this sense they were true
331 (rheotrophic) swamps and coal deposition was associated with frequent
332 influxes of siliciclastics. In late Albian to Coniacian times, however, seams are
333 commonly several metres thick with low ash contents. Chemical and
334 palynological analyses suggest internal nutrient cycling and a gradual
335 reduction in diversity as mire development progressed (Youtcheff et al.,
336 1987). Taken together these signatures are indicative of raised (ombrotrophic)
337 mires maintained by high rainfall. High precipitation, however, did not prevent
338 frequent, low intensity, short duration wildfires as evidenced by numerous
339 millimetre-scale fusain (charcoal) horizons throughout the coals. Peat
340 accumulation was also supported by high summer productivity coupled with
341 temperature-mediated minimal decay of shed organic material during the
342 winters (Spicer et al., 1992).

343 Plant megafossils from the Tuluvak Formation (the [Tuluvak Tongue] of
344 the now revised Prince Creek Formation), central North Slope (Fig. 4), occur
345 in upper alluvial plain bentonitic clays, siltstones and coals and are best
346 preserved in siltstones and siderite nodules within the clays. They are
347 regarded as Coniacian in age based on marine biostratigraphic control
348 (Brosgé and Whittington, 1966; Gryc et al., 1951; Mull et al., 2005) as well as

floral composition. The palaeolatitude, based on Nanushuk palaeomagnetic determinations (Witte et al., 1987) and plate reconstruction of (Smith et al., 1981) has been estimated at 75 °N, but could be higher (Fig. 1). Leaf margin analysis (LMA) of Coniacian Alaskan material suggests mean annual temperatures (MATs) may have been as high as 13 °C (Parrish and Spicer, 1988a), while an early multivariate foliar physiognomic study suggests a MAT of 12.5 °C with a warm month mean temperature (WMMT) of 20.0 °C and a cold month mean temperature (CMMT) of 5.7 °C (Herman and Spicer, 1997). Coniacian standing forests are known from northern Alaska, although anatomical details of the stumps are poorly preserved (unpublished personal observation by RAS). Angiosperms show a mixture of toothed “platanoid” forms and entire-margined taxa that await formal description but are illustrated in Herman and Spicer (1997).

Northern Alaska woody angiosperm floral diversity, like that of the late Cenomanian, was high, but then declined throughout the remainder of the Late Cretaceous as a consequence of increased specialisation and taxonomic canalisation (Spicer, 1986) coupled with climatic deterioration (Spicer and Parrish, 1987; Spicer, 1987). North Slope palaeobotanical studies of the Late Campanian to latest Maastrichtian parts of the Prince Creek Formation [Kogosukruk Tongue] (palaeolatitude 83 - 85 °N) indicate that the MAT was between 2.5 and 5 °C (Spicer, 1987; Parrish and Spicer, 1988a), summer temperatures were lower than in the Cenomanian and Coniacian, and tree ring data suggest that intra- and inter-annual environmental variation was marked (Spicer and Parrish, 1990a). Angiosperm leaf diversity from Alaskan North Slope Maastrichtian localities is too low to attempt a multivariate

physiognomic analysis so estimating winter temperatures is problematic, but again there is no sedimentary evidence for periglacial conditions at, or near, sea level and no frost rings have been observed in fossil trees.

To the south in Denali National Park Tomsich et al. (this volume) report on a lower Cantwell Formation Maastrichtian floral assemblage that is more diverse consisting, primarily, of taxodiaceous conifers, ferns, *Equisetites*, rare ginkgophytes and cycad fragments together with a woody angiosperm component sufficient for a CLAMP analysis. The composite flora yields a MAT of 7.4 ± 2.4 °C, a WMMT of 17.1 ± 3.2 °C and a CMMT of -2.3 ± 3.8 °C. The growing season was just 4.8 ± 1.4 months (all uncertainties here are 2 standard deviations of the residuals about the calibration regressions).

Increasingly abundant fossil charcoal and a diminution of coal abundance and quality suggests later Cretaceous vegetation experienced frequent wildfires and, although mud cracks are absent from the sedimentary record (Phillips, 1987, 1988, 2003), the annual distribution of precipitation may have been less uniform than in the mid Cretaceous.

Pollen data from the Maastrichtian parts of the Prince Creek Formation reveals a higher diversity of angiosperms than is evident from the megafossils (Frederiksen et al., 1988) and the spatial and stratigraphic heterogeneity are indicative of herbaceous types, probably insect pollinated, with a short life cycle and rapid evolutionary turnover. Trees were small in the latest Cretaceous (Spicer and Parrish, 1987; Spicer and Parrish, 1990b) with forests probably being more open and dominated by deciduous taxodiaceous conifers such as *Parataxodium wigginsii* Arnold and Lowther. This taxon is similar to modern *Metasequoia*, but regarded as sufficiently distinct to warrant

a separate genus (Arnold and Lowther, 1955). Ferns and *Equisetites* still were common as ground cover but herbaceous, possibly annual, flowering plants were also abundant. Overall the vegetation structure may have approached that of modern Taiga and been similar in structure to that seen in central Alaska today. Some rare occurrences of the wood type known as *Xenoxylon latiporosum* (Cramer) Gothan in the late Maastrichtian of northern Alaska exhibit ring characteristics similar to those of the Cenomanian and may be indicative of short-lived warm episodes just prior to the end of the Cretaceous. Such Maastrichtian warming episodes have been reported from lower latitudes in N. America (Wolfe and Upchurch, 1987).

3. Cretaceous Floras from Northeastern Russia

As far as can be determined, non-marine floristic successions from N.E. Russia have much in common with those of Alaska, but critical to any North Pacific/Arctic regional studies of vegetation patterns and climate change is reliable correlation facilitated by precise dating. Cretaceous floras from northeastern Russia (Figs. 5 and 6) exhibit much the same vegetational composition as those in Alaska (e.g. Lebedev, 1976; Samylina, 1974; Herman, 1991; Herman, 1993; Herman and Lebedev, 1991; Herman and Shczepetov, 1991; Samylina, 1973; Shczepetov, 1991; Spicer et al., 2002b), although the flowering plants may appear slightly earlier.

Pre-angiosperm floras are in the most part conifer-dominated and typified by the Aptian Silyap and the Albian Buor-Kemyus regional palaeofloras (Fig. 5). Most relevant to Alaska is the Buor-Kemyus floral type

known from several locations, the richest being the Buor-Kemuss Formation of the Zyrianka Coal Basin (Kolyma River Basin: Prynada, 1938; Samylina, 1964; Samylina, 1967), the upper subformation of the Ainakhkurgen Formation and the Chimchememel Formation of the Ainakhkurgen Depression, Bolshoi Anui River basin (Filippova, 1975; Samylina, 1976), the Umkuveem, Marakveem and Irvunei Formations of the Umkuveem Depression, Yeropol River basin (Filippova, 1975; Samylina, 1976) and the middle and upper subformations of the Omsukchan and Toptan Formations of the Omsukchan area near Magadan (Samylina, 1976).

The Buor-Kemyus regional palaeoflora is characterised by fern-rich associations (typically with *Osmunda*, *Birisia*, *Coniopteris*, *Arctopteris*, *Cladophlebis*, *Hausmannia*, *Asplenium*, *Onychiopsis*, *Adiantopteris*, etc.) forming the ground cover together with sphenophytes (*Equisetites*) and cycadophytes (*Nilssonia*, *Nilssoniopteris*, *Anomozamites*, *Neozamites*, *Heilungia*, *Butefia* and *Taeniopteris*). Larger stature plants are represented by the czekanowskialeans (leaf taxa *Czekanowskia* and *Phoenicopsis* together with the reproductive structure *Leptostrobus*). Both 'ancient' conifers (*Podozamites* and *Pityophyllum*) together with conifers of a more modern aspect (e.g. *Sequoia*, *Cephalotaxopsis*, *Pityostrobus*, *Pityospermum*) made up the forest canopy in late seral stages. In total over 150 species have been reported as comprising the Albian Buor-Kemyus flora to which the 57 species found in the Kukpowruk flora have been compared (Spicer and Herman, 2001).

Correlative with floras of the widespread Buor-Kemyus type are those of the Early Ginter regional palaeoflora (Fig. 6) of northeastern Russia. This is

typified by the assemblages of the Ginter Formation at Ugol'naya Bay that occur below a 330 m thick marine unit containing the Cenomanian *Inoceramus pennatulus* zone (Herman, 2007a). Early Ginter floras lack angiosperms and have a prevalence of taxa characteristic of the Early Cretaceous such as *Hausmannia* ex gr. *bilobata* Pryn. *Cladophlebis* aff. *williamsonii* (Brongn.) Brongn. *Sagenopteris*, *Neozamites* (?) and *Podozamites*.

[Figure 6 near here]

Herman and Spicer (this volume) correlate the K-Ar dated (Kuzmichev et al., 2009) late Albian Balyktakh Flora of Novaya Sibir Island with both the N.E. Russian Buor-Kemyus Flora and the late Albian to Cenomanian Kukpowruk Flora of western North Slope, Alaska (Smiley, 1969b; Spicer and Herman, 2001).

Previous non-marine stratigraphy in N.E. Russia, and by extension to some extent other parts of the Russian Federation, was in part based on floral correlation with the Yukon River assemblages of the now abandoned Shaktolik Group (Hollick, 1930). Krassilov (1975) assumed an Albian age for the Yukon Floras and used this to date many eastern USSR floras. However Spicer (1983) showed that the Yukon assemblages were late Cenomanian (cut into by some Turonian (?) channels) and correlative with the Cenomanian [Niakogon Tongue] of the Nanushuk Formation.

Also coeval with the Nanushuk is the highly diverse (84 angiosperm taxa) taphoflora of the Yelisseev locality along the banks of the Grebenka

474 River (Filippova, 1979, 1988, 1989; Herman and Spicer, 1999; Spicer et al.,
475 2002a) that typifies the Grebenka regional palaeoflora found throughout N.E.
476 Russia (Figs. 5 & 6). Deposited rapidly at palaeolatitude 72 °N on the
477 floodplains to the south east of the Ochotsk-Chukotka Volcanic Belt (OCVB)
478 highlands, assemblages at the Yelisseev locality have been $^{40}\text{Ar}/^{39}\text{Ar}$ dated as
479 96.8 Ma and are thus Cenomanian in age (Spicer et al., 2002). This age
480 determination is consistent with biostratigraphic dating of marine units above
481 and below the plant bearing succession that lies within the Krivorechenskaya
482 Formation, as well as floristic and palynological studies (summarised in Spicer
483 et al., 2002).

484 Regionally the Grebenka floral type is highly diverse with over 200
485 taxa, of which angiosperms typically make up 35-40%, and conifers and ferns
486 20-25%. Locally fern remains dominate the assemblages. Oversupply of
487 volcanoclastic sediments to the Grebenka (Yelisseev locality) ancient
488 floodplain led to a dynamic sedimentation regime that captured and preserved
489 plant remains deposited in a suite of different settings. This has allowed
490 detailed reconstruction of the seral development of this vegetation, as well as
491 its composition and structure. Material retrieved from the Yelisseev site is
492 dominated by angiosperms, which comprise more than 50% of the species
493 present, followed in order of decreasing diversity by conifers, ferns,
494 sphenophytes etc.. *Menispermites*, *Platanus*, *Araliaephyllum*,
495 *Scheffleraephyllum*, *Dalembia*, and *Grebenkia* are the most abundant
496 angiosperm genera. Less abundant are *Trochodendroides*, *Diospyros*,
497 *Myrtophyllum* and *Cissites*, and several fossil leaves of dicots that are
498 tentatively assigned to the form genus *Dicotylophyllum*.

499 Entire-margined leaves (*Magnoliaephyllum*, *Myrtophyllum*,
500 *Scheffleraephyllum*, etc.) are surprisingly numerous given that these are
501 usually associated with warm climatic regimes (Bailey and Sinnott, 1915,
502 1916; Wilf, 1997; Wolfe, 1979). Lobed (*Platanus*, *Cissites*, *Menispermities*,
503 *Araliaephyllum*) and compound (*Scheffleraephyllum*, *Dalembia*, *Sorbites*,
504 *Sapindophyllum*) forms also occur.

505 The mesic conifer foliage form *Cephalotaxopsis*, especially *C.*
506 *intermedia*, predominates over the more xeromorphic *Araucarites*, *Elatocladus*
507 and *Pityophyllum*. Shoots of *Araucarites anadyrensis* are commonly found
508 associated with elongate female cones and with tree trunks up to 40 cm in
509 diameter. *Florinia*, *Pagiophyllum*, *Tollia*, and *Sequoia* also occur. Like
510 *Araucarites*, *Pagiophyllum triangulare* represents shoots with rigid scale-like
511 leaves and, based on its morphology, is likely to have been evergreen.

512 *Coniopteris* and *Birisia* are the most ubiquitous ferns, with *Gleichenia*,
513 *Gleichenites*, *Hausmannia*, *Arctopteris*, *Asplenium* and *Cladophlebis* also
514 being common.

515 Cycadophytes are numerous and the deciduous shoot-shedding
516 *Nilssonia* is the most diverse among them. Bedding planes occasionally have
517 abundant leaf accumulations of *Nilssonia alaskana* and *Cycadites*
518 *hyperborea*. A short shoot of *Nilssoniocladus chukotensis* Spicer et Herman
519 with three *Nilssonia* leaves attached has been found at the locality (Spicer
520 and Herman, 1996). *Taeniopteris* remains occur but are not common.

521 Remains of the Ginkgoales, i.e., the genera *Ginkgo* and *Sphenobaiera*,
522 are found frequently, whereas *Pseudotorellia* (?) fossils are rare.

523 Czekanowskiales are represented by very rare impressions of *Phoenicopsis*

524 ex gr. *angustifolia*, and the Caytoniales by the polymorphic leaflets of
525 *Sagenopteris*.

526 The pattern of seral development in the Grebenka Flora may be
527 summarized as beginning with the putative bryophytes *Thallites* and
528 *Marchantites* colonizing bare moist sub-aerial sediment, and the fern
529 *Hausmannia* growing in ponds and lakes. As with earlier pre-angiosperm
530 floras *Birisia* and *Equisetites* formed an herbaceous ground cover community.
531 On drier substrates *Birisia* was, typically, then joined by the fern *Coniopteris*
532 and sometimes by *Glechenites*. Significantly this seral stage included woody
533 deciduous flowering plants represented by the leaf genera *Platanus*,
534 *Grebenkia* and more rarely *Sheffleraephyllum*. Deciduous *Ginkgo* and
535 *Nilssonia* formed subordinate components. In wetter sites *Cycadites*
536 dominated this seral stage.

537 *Coniopteris*, *Birisia*, *Nilssonia*, *Grebenkia*, *Sheffleraephyllum* and
538 *Ginkgo* then persisted while being joined by the conifers *Cephalotaxopsis* and
539 *Elatocladus smittiana*, and the angiosperms *Araliaphyllum*, *Menispermities*
540 and *Dalembia*. *Cephalotaxopsis* and *E. smittiana* then went on to dominate
541 the community with *Pityophyllum* as an occasional subordinate component.
542 Loss of diversity at this stage suggests, perhaps, closure of the canopy. In
543 drier sites the xeromorphic conifers *Pagiophyllum*, *Araucarites* and *Sequoia*
544 *reichenbachii* finally dominate the mature forest community. These taxa are
545 not present in wetter environments, which are typified by *Cephalotaxopsis* and
546 *Elatocladus*. Evidence for this seral interpretation and illustrations of the foliar
547 forms are given in Spicer et al. (2002).

Many of the Grebenka taxa are common to the Nanushuk and our understanding of the Grebenka vegetation structure and dynamics (seral development) also applies to floras of the Nanushuk Formation. One noticeable difference, however, is that the most mature Grebenka forests contain a high proportion of microphyllous and xeromorphic conifers (e.g. *Pagiophyllum* and *Araucarites*) that may well have been evergreen. These forms are not characteristic of the Nanushuk vegetation where only very rarely microphyllous cupressaceous forms (likely to have been evergreen) are found. This may be indicative of a slightly lower palaeolatitude (72 °N) and/or lower winter temperatures because cold depresses respiratory metabolic rates and makes retention of leaves an energetically viable strategy for overwintering (Herman and Spicer, 1999).

It is unlikely that the Nanushuk floodplain was a more disturbed environment (thereby preventing the establishment of mature forests) because the Grebenka succession shows evidence of rapid deposition and dynamic changes in fluvial regime (Spicer et al., 2002). Edaphic factors were likely also to have been important here in that the highly volcanoclastic, predominantly coarse-grained, Grebenka suite of sediments may, overall, have included plant material derived from sites with a similar coarse substrate that were better drained than on the Nanushuk alluvial plain where ash falls were finer grained and consequently less permeable.

Previous palaeoclimatic reconstructions for the Grebenka Flora as a whole suggest a MAT of 13 °C, a WMMT of 20.8 °C and a CMMT of 5.5 °C. Because this is one of the most diverse Late Cretaceous Arctic angiosperm floras (84 morphotypes) and was deposited rapidly (probably <100 kyr) it is

573 regarded as one of the most reliable palaeoclimatic determinations. For a
574 detailed account of the flora, age determination and sedimentary context see
575 Spicer et al. (2002).

576 An intriguing, important, but under-studied Russian flora that post-
577 dates both the Nanushuk and Grebenka Floras is that of the Turonian
578 Derevyannye Gory Section on Novaya Sibir' Island. The sedimentary
579 succession is rich in volcanoclastics, lacustrine deposits and unconsolidated
580 peats and contains an abundant and diverse flora of about 50 species
581 belonging to 33 genera made up of angiosperms, conifers, ferns and
582 ginkgophytes. This, together with the nearby Albian Balyktakh Formation of
583 Kotel'nyi Island, probably represents the warmest, highest latitude, floras of
584 the Cretaceous. Previous palaeoclimatic interpretations of this flora based on
585 20 angiosperm morphotypes suggested a MAT of 9 °C, a WMMT of 18.5 °C
586 and a CMMT of 0 °C. (Herman and Spicer, 1997). A more complete and
587 revised treatment is presented in Herman and Spicer (this volume).

588 As with that of the Grebenka River, another Russian floral assemblage
589 that exhibits a relatively high proportion of xeromorphic elements is the
590 Chauna (sometimes referred to as the Palyavaam) Flora. Originally regarded
591 as 87-100 Ma in age based on Rb-Sr dates and phyt stratigraphy (Belyi,
592 1977; 1997; Samylina, 1988) it is floristically distinct from other floras from
593 N.E. Russia and thus its age and correlation with other floras in the region has
594 proved somewhat problematic. Despite this, Samylina (1974; 1988) proposed
595 a late Albian age based on the presence of Early Cretaceous forms such as
596 *Tchaunia*, *Kolymella*, various species of the fern *Cladophlebis*, *Sphenobaiera*,
597 *Ctenis*, *Heilungia*, *Phoenicopsis*, *Elatocladus* and *Araucarites*, mixed with

598 some younger taxa that appear in the Late Cretaceous such as *Picea*,
 599 *Sequoia* cf. *reichenbachii*, *Menispermites* and *Ziziphoides*. Belyi (1977; 1997)
 600 suggested it was correlative with floral zone II of the Chandler River
 601 succession (Smiley, 1969a), in Northern Alaska. Shczepetov (1991) proposed
 602 a younger Cenomanian to Turonian age, but subsequently revised his
 603 estimate to “early Late Cretaceous”. The Chauna volcanic sediments have
 604 since been $^{40}\text{Ar}/^{39}\text{Ar}$ dated using plagioclase feldspar, biotite and amphibole
 605 (Kelley et al., 1999). All measurements lie within 2_ errors of each other and
 606 yield a mean age of 88 Ma, and therefore are indicative of a Coniacian age
 607 (Gradstein et al., 2005). This is more consistent with the angiosperm
 608 component of the flora that, as well as *Menispermites* and *Zizyphoides*,
 609 contains *Cinnamomoides*, *Trochodendroides*, *Quereuxia* and leaves included
 610 in the form genus *Dicotylophyllum*, all of which are indicative of a mid Late
 611 Cretaceous age. The original dating partly arose because of the highly
 612 endemic nature of the flora, the uniqueness of which is possibly due to the
 613 highly volcanoclastic nature of the palaeosols and thus is primarily edaphic.
 614 There is also the possibility that the flora was deposited at moderate elevation
 615 within the Ochotsk-Chukotka volcanic highlands (Kelley et al., 1999).

616 The Arman Flora comes from terrigenous and volcanoclastic deposits of
 617 the Arman and Naraula formations of the OCVB in N. E. Russia. According to
 618 its systematic composition it is Turonian-Coniacian in age (Herman, 2004).
 619 $^{40}\text{Ar}/^{39}\text{Ar}$ data provide similar results in that the Naraula Formation has been
 620 variously dated as 86 ± 1 , 85.6 ± 1.3 and 85.5 ± 1.1 Ma (Hourigan and Akinin,
 621 2004), whereas U-Pb SHRIMP analysis of zircons from the Arman Formation
 622 yields an age of 92 ± 2 Ma (Akinin, 2007). The Arman Flora has so far been

shown to contain about 80 species of sphenophytes, ferns, ginkgoaleans, czekanowskialeans, conifers and angiosperms, with *Birisia ochotica* (a fern) and *Podozamites*, *Cephalotaxopsis* and *Sequoia* (conifers) being the most abundant. Among angiosperms (26 species), *Araliaephyllum*, *Scheffleraephyllum*, *Dalembia*, *Menispermities*, *Trochodendroides*, *Ziziphoides* and platanoid leaves are numerous. In terms of systematic composition the Arman Flora is similar to the Turonian Kaolak Flora and, to a lesser extent, to the Coniacian Tuluvak Flora of northern Alaska.

Recently (Belyi, 2008) has argued that discrepancies between isotopic dates and geological data within the OCVB means that the isotopic systems clock might have been reset in the region, particularly in respect of $^{40}\text{Ar}/^{39}\text{Ar}$ and U-Pb (SHRIMP) methodologies, and that it is premature to abandon the older chronostratigraphic framework. He cites, amongst other data, the mismatch between regionally obtained Rb-Sr dates ranging from 104 ± 3 to 93 ± 5 Ma (Kotlyar and Rusakova, 2004) and the $^{40}\text{Ar}/^{39}\text{Ar}$ and U-Pb (SHRIMP) results (e.g. Akinin et al., 2006; Akinin and Khanchuk, 2005; Hourigan and Akinin, 2004; Ispolatov et al., 2000; Kelley et al., 1999; Tikhomirov et al., 2006) that tend to yield younger ages. Given the known susceptibility of the Rb-Sr system to chemical alteration this mismatch is not too surprising, but clearly more detailed isotopic work needs to be conducted in the area to resolve the disparities.

Additional angiosperm-rich floras on the margin of the OCVB come from the Northern Pekulney Range (Craggs, 2005; Terekhova and Filippova, 1983; Terekhova and Filippova, 1984) in the Anadyr-Koryak region of N.E. Russia. Two main assemblages are known: the Tylpegyrgynai and the

648 Poperechnaya, named after the formations in which they occur, and both
649 suggest a predominantly deciduous phenology with few evergreen elements.
650 The compositions of these assemblages are similar, but sufficiently different
651 for them to be treated separately (Craggs, 2005). Both are considered to be
652 early Coniacian in age based on biostratigraphy of the underlying (in the case
653 of the Poperechnaya) and overlying (for both the Poperechnaya and
654 Tylpegyrgynai Formations) marine units (Fig. 6). The Tylpegyrgynai
655 assemblage is dominated by angiosperms (40% of taxa) with less diverse
656 conifer and fern components. Cycadophytes, ginkgophytes, sphenophytes,
657 lycopods and probably liverworts complete the plant spectrum. The
658 Poperechnaya assemblage is even more angiosperm dominated (50% of
659 taxa), but otherwise the composition is similar to that of the Tylpegyrgynai
660 Formation. For a full account of the Northern Pekulney Range floras see
661 (Craggs, 2005). A comprehensive analysis of the angiosperm morphotypes is
662 given on the CLAMP website ([http://www.open.ac.uk/earth-](http://www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html)
663 [research/spicer/CLAMP/Clampset1.html](http://www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html)).

664 The Vilui Basin in central Siberia accumulated sediments throughout
665 the Late Cretaceous providing a window into continental interior high latitude
666 palaeoenvironments at that time. The abundant flora (Budantsev, 1968;
667 Vakhrameev, 1958; Vakhrameev and Pushczarovskii, 1954) has been
668 collected from the Timerdyakh Formation, the sediments of which are typically
669 channel sandstones interbedded with floodplain silts and clays,
670 autochthonous coals and stacked palaeosols (Spicer et al., 2008). This is an
671 exceptionally diverse flora with over 170 pollen and spore taxa of which 61
672 are spores (at least 33 represent ferns), 14 are gymnosperm pollen, 10 are

from monocots (including two probable primitive palms) and approximately 90 are pollen from dicot flowering plants. The grains are well preserved (Hoffman and Zetter, 2007) and no more than 10% appear to have been reworked from older sediments. Some of the diversity is a result of the long time interval over which the formation was deposited (latest Albian to Maastrichtian) and the fact that even very small ($<10\mu\text{m}$) grains were recovered by not sieving the preparations. Nevertheless the Cenomanian megafossil floras from the banks of the Tyung River are also diverse and previous analyses of the dicot leaves indicated a MAT of $13.1\text{ }^{\circ}\text{C}$ and WMMT of $21.1\text{ }^{\circ}\text{C}$ and CMMT of $5.8\text{ }^{\circ}\text{C}$. These temperatures are consistent with the overall composition of the flora and the clay mineralogy. Based on weak magnetisation of the Timerdyakh sediments a palaeolatitude of $71.5 - 73.2\text{ }^{\circ}\text{N}$ has been suggested (Spicer et al., 2008) but the Scotese reconstructions estimate a slightly lower palaeolatitude of $68\text{ }^{\circ}\text{N}$. The length of the growing season (daily temperatures above $10\text{ }^{\circ}\text{C}$) is estimated to have been 7.4 ± 1.7 months (Spicer et al., 2008). Despite the continental interior position there is no sedimentological or botanical evidence for freezing.

The Valizhgen Formation from northwestern Kamchatka is made up of coarse-grained sandstones together with sandy-clayey and coaly-clayey shales and contains numerous plant fossils that have been divided into a Coniacian Kayvayam Flora and a Turonian Penzhina Flora (Herman, 1991) (Fig. 6). These were combined with co-eval floras from the Valizhgen Formation on the Yelistratov Peninsula to form separate Coniacian and Turonian Kamchatkan floras, both at palaeolatitudes between 70 and $75\text{ }^{\circ}\text{N}$, that could be used for palaeoclimatic studies. Angiosperm morphotypes used

in these analyses are illustrated in Herman and Spicer (1997). Multivariate physiognomic analysis for the Turonian flora indicated a MAT of 6.9 °C with a WMMT of 17.8 °C and a CMMT of -3.8 °C, while the Coniacian flora was interpreted to have grown under a MAT of 9 °C, a WMMT of 18.6 °C and a CMMT of 0 °C (Herman and Spicer, 1997).

The latest Cretaceous Kakanaut Flora of the Koryak upland region of N.E. Russia (Fig. 6) is of particular interest because of its association with a latest Cretaceous dinosaur fauna, including remnants of eggs (Godefroit et al., 2009). The plant fossil assemblages are richer than those of the co-eval dinosaur-yielding alaskan Prince Creek Formation (Brouwers et al., 1987; Clemens, 1985; Fiorillo and Gangloff, 2000), but not, as claimed by Godefroit et al. (2009) “the richest Cretaceous palaeoflora in the Arctic region”, as will be evident from the works reviewed here. Nevertheless, over 50 megafossil plant taxa have been reported (Golovneva, 1994a; Golovneva, 1994b) including locally abundant *Ginkgo*, and the cycadophytes *Encephalartos* and *Nilssonia* forming monodominant associations. Within the 30 or so angiosperm taxa recognised are *Peculnea*, *Cissites*, “*Corylus*”, *Celastinites*, platanoids, *Trochodendroides* and *Fagopsiphyllum*. Entire-margined forms make up about 15% of the woody flowering plant leaves. Conifers are assigned to the Taxodiaceae, Cupressaceae and Pinaceae. Godefroit et al. (2009) report that of the 10 gymnosperm taxa identified four are regarded as evergreen, but these are not specified.

Previous multivariate physiognomic analysis indicated a MAT of 10 °C with a CMMT between 0 and 6 °C and high rainfall between 1500 and 1700 mm/yr (Golovneva, 2000). The palaeolatitude of the Kakanaut Flora is of

particular importance because the light regime is critical to arguments of dinosaur over-wintering behaviour. Godefroit et al. (2009) cite a position of between 70 and 75 °N based on Howarth (1981) and Smith et al. (1981) and this is supported by the reconstruction shown in Fig. 1. The Smith et al. (1981) reconstruction places the Alaskan Prince Creek localities at a much higher position at around 85 °N, which is consistent with the considerably more depauperate woody flora lacking any discernable evergreen components. In contrast Figure 1 positions the Prince Creek only a few degrees higher than the Kakanaut at about 78 °N. The palaeolatitudinal difference in data supplied by Chris Scotese that form the basis of the latitudinal thermal gradients reported later in this work place the Alaskan Prince Creek locality at 82 °N and the Kakanaut at 76 °N.

4. Floral Interchange and Differentiation in the Cretaceous Arctic

[Figure 7 near here]

The relationships between the regional paleofloras of North Alaska and N.E. Russia are summarised in Figure 7. The similarities, even at the species level, between the Early Ginter and the Kukpowruk, and the Grebenka and Niakogon regional paleofloras indicate a high degree of genetic connection and similarities in climatic regime between the two regions. By the Coniacian (and possibly as early as the late Turonian) a strong differentiation had arisen between the Kaivayam and Tuluvak regional paleofloras. This suggests limited genetic connection and/or climatic differentiation. This persists

throughout the Coniacian and on to the Maastrichtian. The Koryak floral type spans the end Cretaceous transition to the Paleocene and this continuance is indicative of a notable lack of extinctions at these high palaeolatitudes (Spicer et al. 1994; Herman, 2007c). After the K/T transition warming at high Arctic latitudes led to an early Paleocene poleward migration of many taxa such that the early Sagwon Flora of North Alaska (Selandian-Thonetian) (Spicer et al., 2009b) shows strong similarities with the Maastrichtian Koryak Flora (Moiseeva et al., 2009).

[Figure 8 near here]

5. Lower Latitude Floras

As well as the Arctic floras considered here, a small selection of lower latitude floras from the Tethyan margin and N. America have been analysed to derive latitudinal temperature gradients and thus to suggest near polar climatic regimes where plant diversity is otherwise too low for reliable “in situ” analyses.

5.1 North America

The late Jack A. Wolfe scored several Late Cretaceous floras from North America but as yet they are unpublished. His scores for the Tuscaloosa, Woodbine, Lance, Ripley, Gayhead, Cooper and Edmonton floras (Fig. 1)

were used for the analyses reported here. The ages and palaeolatitudes used to derive the latitudinal temperature gradients are given in Figure 9.

5.2 Europe

The positions of these sites are given in Figure 1. Leaves from two localities within the Peruc Flora, Czech Republic (Vysehorovice and Praha Mala Chuchle), represent florules of the same Cenomanian age, but different environments (Herman et al., 2002). Plant fossils from the Praha Mala Chuchle locality come from the fluvial sediments deposited in a Cenomanian river channel bordered by slopes of Palaeozoic limestone bedrock, whereas those from the Vysehorovice locality come from fluvial sediments of a larger river meandering across an extensive lowland floodplain. CLAMP analyses of these florules are presented separately and in combination (Peruc). Also from the Czech Republic is Senonian flora of Zliv, Klikov and Hluboka (Nemejc, 1962; Nemejc and Kvaek, 1975; Herman et al., 2002; Váchová and Kvaek, 2009), which are here combined and labelled “Czechsen” in Table 1.

The Campanian Grünbach Flora comes from the Grünbach Formation of the Gosau Group in the Grünbach-Neue Welt Basin in the Eastern Alps, Austria (Herman and Kvaek, 2007a, b, 2009). The probable early Campanian age of this flora is based on the correlation of plant-bearing deposits with marine biostratigraphy and on palynological data (Summesberger, 1997). The palaeogeographic situation is that of a large island with unknown relief on the northern margins of the Tethys Ocean. Terrestrial freshwater swamps and shallow water sediments indicate a relatively large deltaic plain. Lithological

climate indicators, as well the presence of large foraminifers, rudists, corals and a reptile fauna (carnosaurs, iguanodons, pterosaurs, scelidosaur and crocodiles) throughout the Santonian-Maastrichtian of the Grünbach Basin, suggest a 'subtropical' climate considerably warmer than that experienced in the Arctic. As well as a diverse fern, conifer and dicot flora the plant assemblage contains early palms and *Pandanus* (Herman and Kvaček, 2009). An end Cretaceous palaeolatitude of 32 °N for the Gosau Basin has been reported (Preisinger et al., 1986).

6. Quantifying Non-marine Circum-Arctic Palaeoclimates

Earlier palaeoclimate determinations have been a combination of qualitative and quantitative analyses. Qualitative interpretations have included those of tree rings (Parrish and Spicer, 1988b; Spicer and Parrish, 1990b), vegetational composition (Spicer and Parrish, 1986), and interpretations of shoot and leaf architecture coupled with taphonomic observations (Spicer and Herman, 1996) and floral diversity (Smiley, 1967). These have constrained the light regime and seasonality as well as indications of evaporation / precipitation ratios, overall precipitation, and, to some extent, air temperatures. Quantitative estimates of mean annual temperatures have been derived from leaf margin analysis (Parrish and Spicer, 1988a; Spicer and Parrish, 1990a) but this technique can offer no indication of seasonal variations in temperature, which is a critical parameter at high latitudes. More latterly, multivariate analysis of foliar physiognomy, specifically Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe, 1993; Craggs, 2005;

Golovneva, 2000; Herman and Spicer, 1996b; Herman and Spicer, 1997; Spicer et al., 2002), has been applied because it can offer estimates of both the warm month mean and cold month mean temperatures as well as seasonal variation in rainfall.

6.1 CLAMP Analysis

Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe, 1993) (<http://www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html>) is a multivariate palaeoclimate proxy based on the observation that leaf architecture is highly responsive to, and reflective of, climate. Leaf architecture (physiognomy) is the result of adaptation within the context of the capabilities of the genome honed by natural selection, and the evolutionary driver is increasing fitness gained by the maximization of photosynthetic capability in the energetically most efficient way. Non-adapted physiognomies do not compete effectively, and over time there is a degree of convergence of form largely independent of taxonomy (Spicer, 2000, 2007, 2008). No single architectural feature of a leaf, or whole plant, determines adaptive success (Lande and Arnold, 1983), and thus no single feature can be expected to correlate with a single climatic variable. It is becoming increasingly clear that numerous interacting traits influence fitness (Ackerly et al., 2000) and architectures of conducting tissues in roots, stems and leaves, overall canopy architecture (Hellicker and Richter, 2008) and foliar physiognomy are all important in producing a photosynthetically efficient structure. However,

because plants rarely fossilise as complete entities, analysis of dispersed organs such as isolated woody stems and leaves is all that is possible.

CLAMP is a non-taxonomic statistical method embedded in well defined calibration and numerically descriptive protocols that attempt an objective decoding of foliar physiognomy in terms of environmental constraints, particularly climate. It has a particular advantage over the so-called Nearest Living Relative methods such as the Co-existence Approach (Mosbrugger and Utescher, 1997) for the Late Cretaceous in that it is grounded in the time-stable laws of the physics of fluid conduction, gas diffusion and radiation balances and therefore can be used in 'deep time' studies where taxon-based evolutionary change is likely. A significant advantage of CLAMP, and most palaeobotanical proxies for that matter, is that unlike isotopic techniques it is not subject to uncertainties arising from diagenetic alteration.

Although non-angiosperms do code for climate in broad qualitative terms (Rees et al., 2000; Spicer et al., 1994), to date quantification is restricted to the physiognomy of woody dicot leaves and can only be applied reliably to floral assemblages where there is a diversity (>20 morphotypes) of such leaves. However such floras provide climatic constraints and insights to Arctic conditions where angiosperms, sufficient in diversity to provide reliable climate estimates, are lacking.

CLAMP is a dynamic methodology that has been periodically improved by, for example, the addition of new modern vegetation calibration (training) sites and the use of different sets of meteorological observations for calibration purposes. Wolfe's (1993) original meteorological data were

gleaned from observations made in, or close to, the vegetation sites used to calibrate the technique and define the structure of multidimensional “physiognomic space”. As such, the observations were to some extent influenced by the presence of the vegetation itself and therefore reflective of the local microclimate and less so the regional climate. Prior to large-scale human destruction of natural vegetation this would not have been a problem, but today climate stations used to amass global climate data are usually located in landscapes highly modified by agriculture and/or urbanisation. These data, on average warmer than those obtained in sub-canopy environments, are those used to evaluate and constrain climate models, and for data/model comparisons for the geological past it is desirable that proxies such as CLAMP use the same meteorological calibration. This is particularly important because there has been a persistent mismatch between palaeoclimate proxies and “warm Earth” model simulations at high latitudes and continental interiors dating back over 25 years (Spicer et al., 2008; Valdes, 2000). Moreover while Wolfe’s calibration data were usually summaries of more than 30 years of observations, the 30 or more years over which the data were collected were not the same.

To achieve a CLAMP calibration more akin to that used in climate modelling we utilized the 0.5° x 0.5° global climate data set of (New et al., 1999) supplemented by the ERA40 re-analysis data for atmospheric temperature at upper levels. The New et al. (1999) data are derived from the World Meteorological Organisation (WMO) 1961-1990 global observed standard normals, supplemented by other data from national meteorological agencies collated by those authors. More detailed accounts of data sources,

standardizations where more than one definition of a climate variable was used, and uncertainties are given in New et al. (1999). To correct for the effect of altitude, a geographically variable lapse rate was calculated by using the 3-D climatology of temperature from the ECMWF re-analysis project (Uppala et al., 2005). From this the mean lower tropospheric lapse rate for each month of the year was calculated. These data are on a 96 x 73 grid that was then interpolated onto a 720 x 360 grid (0.5° x 0.5°) using a bilinear interpolation scheme that conserves area averages. This interpolation scheme inevitably smoothes altitudes and there is no recognition of aspect.

The gridded data were then corrected to the observed altitude of the exact latitude and longitude of the CLAMP calibration site using the monthly lapse rates and a bilinear interpolation scheme. The specific and relative humidities were also recalculated in light of the lapse rates. If the lapse rate corrected temperature was much colder than the original, then potentially the relative humidity could have been greater than 100%. If this was the case, the specific humidity was adjusted until the relative humidity was equal to 100%. From this the commonly returned CLAMP climate variables (mean annual temperature - MAT, warm month mean temperature - WMMT, cold month mean temperature - CMMT, length of the growing season - LGS, mean growing season precipitation - GSP, mean monthly growing season precipitation - MMGSP, precipitation during the three wettest months - 3-WET, precipitation during the three driest months - 3-DRY, specific humidity - SH, relative humidity - RH, and enthalpy) were calculated to provide a meteorological calibration data set (GRIDMET3BR). This was used with the

PHYSG3BRC set of foliar physiognomic scores to provide a calibration framework for the fossil sites. Both are provided on the CLAMP website.

While transferring Wolfe's original hard copy raw scores of the training sets to the electronic score sheet now routinely used in CLAMP analyses, some minor arithmetic errors were detected. While these are so small that they do not materially affect previously published results, they are now corrected and form the PHYSG3BRC data set used here. A more comprehensive analysis of the new calibration scheme as compared to those used previously is given in Spicer et al. (2009a). Using the new gridded calibration, analyses of Arctic floras are here presented together with selected lower latitude Cretaceous sites.

7. Results

The results of the new CLAMP analyses using the gridded meteorological data (GRIDMET3BR) are shown in Table 1.

[Table 1 near here]

In wet regimes it has long been known that leaf physiognomy is poorly constrained by water availability compared to dry regimes (Wolfe, 1993). At Late Cretaceous high northern latitudes there is ample evidence in the terrestrial realm of an excess of precipitation over evaporation, thus estimates of precipitation must be regarded with great caution, and in any case will be biased towards the growing season. Growing season lengths are shorter for

the high palaeolatitude floras and all are between 5 and 8 months, consistent with the temperature and inferred light regimes.

Because of the difficulties of comparing sites of different ages and at different palaeolatitudes across all meteorological parameters, data from GRIDMET3BR CLAMP analyses of 9 additional sites in N. America (Lance, Gayhead, Tuscalloosa, Woodbine, Ripley, Edmonton, and Cooper) and one from Kazakhstan (Teretki-Sai) were added to the results reported here to derive latitudinal MAT gradients. These are shown in Figure 9. WMMT and CMMT gradients were similarly derived, and the R^2 values and standard deviations of the residuals as measures of uncertainty are presented in the legend to Figure 9.

[Figures 9 near here]

Finally, using these gradients it was possible to calculate temperature parameters at any palaeolatitude using the equations of the regressions in Fig. 9. Figure 10 shows the MAT values so derived for 70 and 80 °N superimposed on plots of observed MATs at different times in the Late Cretaceous as derived by different palaeobotanical methods.

[Figure 10 near here]

8. Discussion

968 CLAMP has already been shown to have parity with open water coastal
969 SSTs derived from oxygen isotope analyses from the Cenomanian of New
970 Zealand (Kennedy et al., 2002), and, more indirectly through palaeoelevation
971 estimates, lacustrine bulk carbonate oxygen isotope values (Currie et al.,
972 2005; Spicer et al., 2003). These, and experimental observations (Gregory,
973 1996), suggest CLAMP not only shows reasonable agreement with oxygen
974 isotope proxies, but also that it appears immune (at least within known
975 uncertainties) to calibration errors associated with changing atmospheric CO₂
976 concentrations.

977 Alaskan North Slope Nanushuk Formation palaeosol $\delta^{18}\text{O}$ siderite
978 analyses used the LMA-based temperature estimates of Parrish and Spicer
979 (1988a) for calibration purposes to obtain quantitative estimates of
980 precipitation (Ufnar et al., 2004). The results (485 mm/yr) are consistent with
981 the widespread early Late Cretaceous peat formation (Lottes and Ziegler,
982 1994) and thereby indirectly confirm the palaeobotanical temperature
983 estimates. These early LMA-derived estimates are also consistent with those
984 obtained from CLAMP (although note that CLAMP analyses have yet to be
985 run for Nanushuk Formation floras). CLAMP does, however, yield higher
986 precipitation values than those of Ufnar et al. (2004), particularly bearing in
987 mind that CLAMP estimates growing season precipitation and not mean
988 annual precipitation. These wetter predictions are unsurprising given the high
989 uncertainties associated with foliar physiognomic techniques in wet regimes,
990 and the fact that leaf preservation is biased towards wet depositional
991 environments where the plants would not experience drought-induced water
992 stress.

Overall the new CLAMP values based on the gridded meteorological data calibration are not significantly different from those previously published using Wolfe's (1993) (together with later revisions) calibration data (e.g. Herman and Spicer, 1996b). These, and the earlier CLAMP MAT estimates, are consistent with those obtained by LMA, and show broad agreement with other proxies (Price and Grimes, 2007; Spicer and Corfield, 1992).

8.1 MAT Estimates

Including uncertainties, CLAMP Arctic MAT estimates reported here, and those of Tomsich et al. (this volume), range from around 8 °C to around 15 °C with the coolest conditions (Kamchatka Turonian and Denali Maastrichtian) away from the Arctic Ocean. This is demonstrated most clearly in Fig. 10 where the N.E Russia floras close to the north Pacific are notably cooler than those at similar or higher palaeolatitudes bordering the Arctic Ocean. This is consistent with the post-Cenomanian floral differentiation between the two regions shown in Fig. 7 and supports the idea of a relatively cold northern Pacific Ocean gyre (Herman and Spicer, 1996b), compared to a warmer Arctic Ocean supplied by heat transported northwards along the Western Interior Seaway. Such a phenomenon has recently been seen developing in Late Cretaceous coupled atmosphere/ocean GCMs (P.J. Valdes, personal communication, 2008) and may help explain spatial and temporal heterogeneities in temperature estimates from the circum north Pacific region and elsewhere (Zaharov et al., 1999). Small changes in the position, temperature and intensity of such a gyre would result in significant

differences in temperature proxy estimates depending on their location and accuracy of dating.

Figure 10 also shows good agreement between the Maastrichtian MAT at 80 °N derived using the depauperate floral composition (Spicer and Parrish, 1990) and those projected for the latitude using the CLAMP-derived palaeolatitudinal temperature gradient shown in Fig. 9. The floral estimate is 5 °C as against 6.7 ± 2.2 °C for CLAMP. Note that this uncertainty is obtained from the CLAMP statistical uncertainty (Table 1) and does not incorporate the scatter around the MAT/palaeolatitude regression shown in Fig. 9. When the standard deviation of the residuals is combined with that due to CLAMP methodology the uncertainty remains more or less the same (± 2.23 °C) due to the good fit of the data to the regression.

At 82 °N (the predicted latitude of the Ocean Point locality using the data of Scotese) the MAT is estimated to have been 6.3 °C. This value, and the CMMT, is likely to be cooler than that actually experienced because the slope of the line is influenced by the inclusion of the Cantwell (Denali) data, which is not only derived from the ungridded CLAMP calibration, but is also from a site well away from the Arctic Ocean coast.

Equally intriguing as the cool northern Pacific gyre is the temperature of the Late Cretaceous Arctic Ocean. With the possible exception of seasonal winter ice cover in the Maastrichtian, most authors agree that the Late Cretaceous Arctic Ocean was ice-free year round. This is despite the lowered surface salinity arising from high precipitation in the circum-Arctic region, and restricted connections with the rest of the global oceanic system. Clear signatures of ice (as opposed to tree root) rafting of drop-stones are absent.

1043 Some authors (Jenkyns et al., 2004) have suggested that the average Arctic
1044 Ocean surface temperature at 70 Ma was 15 ± 1 °C and was above 20 °C in
1045 the Cenomanian. These temperatures were arrived at by using the TEX₈₆
1046 proxy based on the composition of membrane lipids derived from marine
1047 plankton belonging to the Crenarchaeota. The material used was obtained
1048 from drop-stone-free varved Maastrichtian organic-rich sediments recovered
1049 by shallow piston core from the Alpha Ridge. The Cenomanian temperature
1050 was arrived at using the Maastrichtian TEX₈₆ value and a proxy oxygen
1051 isotope curve from the English chalk together with assumptions about a
1052 shallow Cretaceous marine equator-to-pole temperature gradient.

1053 To help support their conclusions Jenkyns et al. (2004) cited an 1890
1054 reference to a putative Cenomanian *Artocarpus* (breadfruit) from Greenland
1055 (Nathorst, 1890). It is worth noting that in the 19th and early 20th centuries it
1056 was common practice to name leaves by reference to morphologically similar
1057 extant forms. As our understanding of early angiosperms improved this
1058 practice was abandoned and names distinct from modern genera were used
1059 instead. To assume the Greenland leaf represented a thermophyllic tropical
1060 plant, and to cite the temperature range of 15 - 38 °C under which modern
1061 breadfruits grow as evidence for a tropical Arctic regime, is to ignore evolution
1062 and the overall temperate character of the hundreds of taxa that comprise the
1063 circum Arctic Cretaceous floras. The highly seasonal growth regimes at high
1064 latitudes is likely to bias the TEX₈₆ proxy towards lipids produced in the
1065 warmer summer season and thus the temperatures obtained will reflect the
1066 WMMT rather than the MAT. The Jenkyns et al. (2004) estimates must

therefore be regarded as overly warm in the absence of additional supporting information.

If the Arctic Ocean was warm, and it would be imprudent to take the TEX₈₆ values at face value, how warm was it? Early attempts to use oxygen isotopes to estimate Cretaceous Arctic Ocean SSTs suffered from both an imperfect understanding of the effects of diagenesis and, more importantly, problems associated with reduced salinity.

To avoid salinity uncertainties an alternative approach to estimating polar temperatures is to examine terrestrial equator-to-pole temperature gradients. Moreover, to test the palaeobotanical proxies this gradient should be derived independently of plant fossils. Using oxygen isotope ratios in vertebrate phosphate, including dinosaur bone remains from Alaska, Amniot et al. (2004) constructed a Campanian-Maastrichtian latitudinal temperature gradient that showed good agreement with quantitative palaeobotanical data across almost all the latitudinal range down to 30° (Wolfe and Upchurch, 1987; Parrish and Spicer, 1988a), although the Alaskan isotopic MAT was reported as −5 °C. This is colder than palaeobotanical estimates, but within the thermal tolerance of the inferred Taiga-like palaeovegetation. Given the lack of sedimentological evidence for freezing this figure of −5 °C may be too cold, but not by much, and it is within the 2σ uncertainty range about the −2.3° CMMT CLAMP values obtained by Tomsich et al. (this volume). Taking into account uncertainties in palaeolatitudes, together with those inherent in the methodologies, the plant and isotope proxy data are in good agreement.

For the highly seasonal Arctic, with prolonged periods of darkness, MATs are only part of the story. CLAMP-derived CMMTs attest to a general

lack of freezing conditions and even the coldest CMMT estimates from the Cenomanian and Turonian of the Russian Far East, on the borders of the OCVB, suggest only brief periods (several weeks at most) of mild frosts. Even in the more continental interior position of the Vilui Basin away from oceanic influences, but above the palaeo-Arctic Circle, there appears to have been a lack of freezing during the winters (Spicer et al., 2008). Temperatures bordering the Arctic Ocean (8 °C for the Alaskan Coniacian and 1 °C for Novaya Sibir' Island, Table 1) are consistent with an Arctic Ocean surface temperature well above freezing, and possibly as high as 6 - 10 °C in the Coniacian. Such temperatures are required to maintain warm air temperatures during the prolonged winter darkness.

8.2 CMMT Estimates

A major advantage of CLAMP is that it not only yields MATs but also provides data on mean annual range of temperature. It is reasonable to ask, however, how reliable CLAMP is in estimating the CMMT when plants are dormant during that part of the year. This ability of CLAMP to provide reasonable CMMT estimates despite deep dormancy and deciduousness has been investigated using modern samples from the Siberian interior (Spicer et al., 2004). Although CLAMP tended to provide CMMT estimates that were somewhat too warm, indications of extreme cold were evident in that CLAMP analysis of modern leaves suggested a CMMT of around -30 °C in locations where the observed was closer to -40 °C. The explanation for CLAMP's ability to estimate CMMT could be that at the critical phase of leaf expansion in the

1117 spring leaf architecture has to be functionally efficient during the steep
1118 warming trajectory from winter to summer temperatures ($>35^{\circ}\text{C}$). The CMMT
1119 physiognomic signal is therefore a reflection of rapid spring change. In the
1120 Cretaceous there would have been an equally, if not more, rapid foliar
1121 development phase driven by a fast-changing light regime and some
1122 associated warming despite the relatively warm winters.

1123 CLAMP climate estimates are consistent with the overall composition
1124 of the Arctic vegetation. Vegetation composition ranged from being
1125 characteristic of warm temperate to cool temperate throughout the Late
1126 Cretaceous. Conditions cold enough to lead to the development of vegetation
1127 similar to that of modern Taiga appear to have existed in the Maastrichtian in
1128 northern Alaska, but even then winter CMMT temperatures may not have
1129 been significantly below freezing. Unfortunately the flora representing the
1130 coolest conditions contained insufficient woody dicot taxa for a CLAMP
1131 analysis, but insights can be gleaned from the gradients obtained lower
1132 latitude co-eval North American floras. Using this approach the estimated
1133 CMMT at 82°N was $-1.98 \pm 3.9^{\circ}\text{C}$ (2σ combined uncertainty). It is likely then
1134 that in the northern Alaska Maastrichtian winter episodes of temperatures $< -$
1135 10°C probably did occur, but were rare and unlikely to have lasted more than
1136 a week or so. Even so winter cold, combined with prolonged darkness and a
1137 lack of foliage for food, would have posed significant problems for the resident
1138 fauna and those that, due to their size, could not have found shelter for
1139 hibernation or aestivation are likely to have migrated south for over-wintering.

1140 In the earlier (warmer) parts of the Late Cretaceous the Cenomanian
1141 CMMT latitudinal gradient was $1.8^{\circ}\text{C}/10^{\circ}$ yielding a CMMT at 82°N of $+3.8 \pm$

1142 4.1 °C (2σ combined) (R^2 0.84, 2σ of residuals 1.96 °C), while in the
1143 Turonian-Coniacian the gradient is predicted to have been 1.4°C/10° with a
1144 CMMT at 82 °N of $+0.2 \pm 5.3$ °C (2σ combined) (R^2 0.47).

1145 By contrast the Cenomanian of the Czech Republic at a palaeolatitude
1146 just above 30 °N show CMMTs between +7.2 and +10.4 °C (2σ uncertainty \pm
1147 3.8 °C; Table 1). Later in the Cretaceous, consistent with the well known Late
1148 Cretaceous global cooling trend, CMMTs decline (Grünbach +3.2 °C and
1149 Czechsen +0.9°C).

1150

1151 8.3 WMMT Estimates

1152

1153 Late Cretaceous Arctic WMMTs suggest cool summers compared to
1154 conditions in Tethyan margin sites (26 - 29 °C). The shallow WMMT latitudinal
1155 gradients of 0.9 °C /10° latitude in the Cenomanian (R^2 0.69, 2σ residuals
1156 1.92 °C), 2.1 °C/10 °C in the Turonian/Coniacian (R^2 0.94, 2σ residuals 1.54
1157 °C) and 2.3 °C /10° latitude in the Maastrichtian (R^2 0.96, 2σ residuals 1.2 °C),
1158 together with those of the CMMT, are consistent with a year-round warmth
1159 and a persistent weak polar high pressure cell. At 82 °N the Maastrichtian
1160 WMMT is projected to have been 14.5 °C with a combined uncertainty (2σ) of
1161 ± 3.1 °C. At 82 °N in the Cenomanian the WMMT is projected to have been
1162 20.5 ± 3.3 °C (2σ combined), while in Turonian-Coniacian it was 17.3 ± 4.8
1163 °C. The difference of 6 °C between Cenomanian WMMT at 82 °N and the
1164 Maastrichtian WMMT at the same palaeolatitude is only marginally greater
1165 than the differences in the CMMTs (5.8 °C) and is certainly not significant
1166 when the uncertainties are taken into consideration. This suggests that

warming and cooling at high latitudes is not just a function of the summer insolation, but reflects changes to the entire annual thermal cycle.

8.4 Humidity and a Permanent Polar Cloud Cap

CLAMP estimates of Arctic annual average relative humidities are all high, being between 70 and 85%. A persistent polar cloud cap has been proposed by Herman (1994), who argued that the large leaf sizes found at high latitudes during the Cretaceous might be a response to diffuse light. Such a cloud cap would also be a product of an enhanced hydrological cycle developed under a weak polar high-pressure cell. Recently Mercado et al. (2009) have shown that the global land carbon sink was enhanced by 23% between 1960 and 1999 due to increased diffuse solar radiation resulting from volcanic sulphur aerosols and “global dimming”. This increase in terrestrial photosynthetic activity resulting from diffuse light would also have operated at high latitudes under the Late Cretaceous polar cloud cap and particularly where extensive and frequent volcanism in the OCVB would have contributed aerosols (see also Herman and Spicer, this volume). Coupled with higher atmospheric CO₂ concentrations and the possible enhancement of evergreen over-wintering strategies under warm dark winters (Royer et al., 2003), this would help explain the high N. polar primary productivity in Late Cretaceous times.

Figure 11 shows a reconstruction of a summer scene under such a cloud cap at 70 Ma on the margins of the Arctic Ocean at approximately 82 °N. Such a year round cloud cap has been generated in some Maastrichtian

coupled ocean/atmosphere modelling experiments using a 3 x pre-industrial atmospheric CO₂ concentration, and a reduced solar constant (run XATTS, unpublished data of P.J. Valdes). In the experiments the CMMT Arctic Ocean margin temperatures over land matched those suggested by the vegetation while the 2 m air temperatures over the ocean were 15 °C. This not only suggests the possibility of very steep thermal gradients from ocean to land, but also that the TEX₈₆ estimates should be regarded as reasonable, despite a likely bias towards the WMMT, pending the emergence of evidence to the contrary.

[Figure 11 near here]

8.5 The Effect of Volcanism

The provenance of the widespread Late Cretaceous bentonites in northern Alaska has long been a contentious issue (e.g., Smiley, 1969a; Bergman et al., 1995) because of the dearth of proximal sources. The first thin Cretaceous bentonites occur in the Albian of the western North Slope. Thick ashes occur later in the Cretaceous, notably in the Cenomanian, and are found further east (Brosgé and Whittington, 1966), although a significant part of Late Cretaceous time is not represented by sediments in the west. ⁴⁰Ar/³⁹Ar ages on biotite and feldspar from tuffs in northern Alaska range from 100 Ma to 67 Ma, but most are 93 - 85 Ma (Bergman et al., 1995); pers. comm. to RAS, 1997). The significance of the Kelley et al. (1999) age reassignment is that it constrains the period of maximum eruptive activity in

1217 the OCVB to coincide with the deposition of the thickest bentonites across
1218 northern Alaska and thus makes it likely that most, if not all, ash deposits in
1219 the Corwin and Umiat Deltas were sourced to the west in N.E. Russia
1220 (Bergman et al., 2006; Kelley et al., 1999) although a Canadian source cannot
1221 be discounted entirely (Bergman et al., 2006). The lack of any ash deposits to
1222 the west of the OCVB constrains predominant Late Cretaceous Arctic wind
1223 directions as being from N.E. Russia eastwards to Alaska. This has
1224 implications for atmospheric heat transport from west to east, and
1225 determinations of air temperatures in N.E. Russia therefore have a bearing on
1226 those in Alaska. Convection over the warm Arctic Ocean coupled with the
1227 rotation of the Earth would have drawn cool air from over the North Pacific
1228 gyre north-eastwards across Alaska leading to offshore winds. This is
1229 reflected in the strong land to sea thermal gradients evident in the XATTS
1230 model run.

1231 The occurrence of ash deposits across the N. Pacific and Arctic Ocean
1232 margin areas raises the possibility that the vegetation, and hence the plant-
1233 derived climate signal, might be compromised by ash-related disturbance.
1234 However studies of modern day eruptions demonstrate that ash falls rarely
1235 cause significant vegetational disturbance in areas distal to volcanic vents
1236 (Spicer, 1989). The lack of vents proximal to northern Alaska suggests
1237 vegetation there was unlikely to have been adversely affected except for
1238 short-term smothering of ground cover. Ash falls undoubtedly contributed
1239 nutrients and stimulated growth in nutrient-poor communities such as on
1240 raised mires. The development of thick palaeosols between ash horizons
1241 suggests long intervals between significant fall events in any given region,

thus the majority of leaf accumulations reflect vegetation minimally impacted by volcanism. Leaf assemblages used in palaeoclimatic analysis were in the most part from siliciclastic horizons with no, or very small, volcanogenic components. The only exception to this was the Grebenka flora at the Yelisseev locality where the volcanoclastics were all fluvially transported from the OCVB uplands and only one ash horizon was found within several hundred metres of section.

In the OCVB frequent heavy ash falls and deep accumulations of volcanoclastics no doubt did affect vegetation composition such as in the case of the Chauna flora (Kelley et al., 1999). Such floras were not used for palaeoclimatic analysis.

9. Conclusions

Despite the Late Cretaceous evolutionary novelty of woody dicots and the lack of any modern analogues for the Late Cretaceous Arctic forests growing under a polar light regime, new CLAMP palaeoclimate determinations using a global gridded climate calibration yield values that are similar to previous estimates using CLAMP, leaf margin analysis, oxygen isotopes based on terrestrial vertebrate phosphates, marine carbonates from the North Pacific and palaeosol siderites. CLAMP values are also consistent with qualitative interpretations arising from plant diversity and vegetation composition, tree rings and clay minerals. This high level of agreement between diverse proxies suggests that CLAMP estimates, although bound to be refined further in the future, are as likely as any method to yield meaningful

1267 climate estimates. To the statistical uncertainties quoted in the CLAMP
1268 methodology have to be added uncertainties arising from palaeolatitudinal
1269 positioning, particularly as latitude is critical to understanding the insolation
1270 regime in near-polar positions.

1271 Palaeobotanical proxies indicate the maintenance of temperatures near
1272 or above freezing over land surrounding the Late Cretaceous Arctic Ocean
1273 despite long periods (possibly as long as 5 months) of continuous darkness
1274 each winter. This argues not only for a persistently warm Arctic Ocean
1275 throughout those months, but an effective thermal “blanket” to keep air
1276 temperatures around the ocean margins high. This is most likely to have been
1277 a more or less permanent polar cloud cap maintained by a strong hydrological
1278 cycle driven by evaporation from the warm ocean. The high precipitation and
1279 humidity values evident from the CLAMP analyses support this, as well as the
1280 precipitation estimates from the palaeosol siderites and the abundance of
1281 coals.

1282 Global cooling towards the end of the Cretaceous, manifest by a
1283 reduction in summer temperatures, was associated with a shallowing and
1284 eventual closure of the Western Interior Seaway and thus a reduction of heat
1285 transport to the Arctic. This may have led to a strengthening of the polar high
1286 and some weakening of the hydrological cycle. This in turn may have reduced
1287 the permanence and thickness of the polar cloud cap compared to earlier
1288 times, and led to further polar cooling and strengthening of the polar high.
1289 Nevertheless, given continued evidence for higher precipitation and
1290 temperatures than today, the cloud cap is likely to have been a feature of the
1291 Arctic throughout the Late Cretaceous and into the Paleocene. Such a cloud

cap can be developed in coupled atmosphere/ocean general circulation models even for the relatively cool Maastrichtian. Ironically events at the end of the Cretaceous such as impact(s) and/or Deccan volcanism may have resulted in a fortuitous interruption of this cooling feedback loop by raising global CO₂ levels and invigorating the global hydrological cycle. The result being Arctic warming most notably expressed by increased plant diversity in the Paleocene palaeolatitudes as high as 85°N (Moiseeva et al., 2009; Spicer et al., 2009b). There is no evidence for major floristic turnover or extinctions at or near the end-Cretaceous boundary. Instead there were migrations into the Arctic as early Paleocene, and possibly late Maastrichtian, warming progressed.

The data presented here further support our earlier suggestion (Herman and Spicer, 1996) that a relatively cool gyre developed in the northern Pacific Ocean during the Late Cretaceous. The effect of the resulting steep temperature gradient between the northern Pacific coastal plains and those of the warmer Arctic Ocean led to taxonomically distinct vegetation developing in these two areas. This differentiation was strongest in mid Late Cretaceous times and only disappeared after the end of the Cretaceous when warming led to migration and re-organisation of Arctic vegetation in the Paleocene.

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1905 252.

1906

1907 Figure Legends

1908

1909 Figure 1. Palaeogeographic reconstructions of the North Polar Region at
1910 100Ma, 88 Ma and 70 Ma based on Hay et al. (1999) and obtained
1911 from the ODSN website (<http://www.odsn.de/>). Plant fossil location
1912 numbers used here and in Table 1 as follows: 1 Coniacian Tuluvak
1913 Formation, 2 Turonian Novaya Sibir', 3 Cenomanian-Turonian Yukon-
1914 Koyukuk Basin, 4 Cenomanian to Maastrichtian Vilui Basin, 5
1915 Cenomanian Grebenka Flora, 6 Turonian Kamchatka, 7 Coniacian
1916 Kamchatka, 8 Turonian-Coniacian Arman River, 9. Coniacian
1917 Tylpergergenai, 10 Cenomanian Chuchle, 11 Cenomanian
1918 Vyshehorovice, 12 Cenomanian Peruc, 13 Campanian Grünbach, 14.
1919 Senonian of the Czech Republic, 15 Albian-Cenomanian Nanushuk
1920 Formation, 16 Albian-Cenomanian Kukpowruk Flora, 17 Maastrichtian
1921 Prince Creek (Kogosukruk) Flora, 18 Maastrichtian Kakanaut Flora, 19
1922 Albian Buor-Kemyus (Zyrianka River Basin), 20 Albian Buor-Kemyus
1923 (Ainakhkurgen Depression), 21 Maastrichtian Lance, 22 Maastrichtian
1924 Medine Bow, 23 Maastrichtian Ripley, 24 Cenomanian Tuscaloosa, 25
1925 Cenomanian Woodbine, 26 Santonian Gayhead, 27 Maastrichtian
1926 Edmonton, 28 Maastrichtian Cooper Pit, 29 Cenomanian Tetetky-Sai.

1927

1928 Figure 2. Map of present day N.E. Russia and Alaska showing positions of
1929 areas yielding taphofloras. 1) Novaya Sibir Island; 2) Arman River; 3)
1930 Yelistratov Peninsula; 4) Cape Valizhgen; 5) Cape Konglomeratoyi; 6)
1931 Grebenka-Orlovka; 7) Chukotskaya-Bystraya River Basin; 8) Ubienka-

1932 Krestovaya River Basin; 9) Chineiveem River; 10) Rarytkin Ridge
 1933 (southwestern part); 11) Pekul'nei Ridge western slope; 12) Pekul'nei
 1934 Ridge eastern slope; 13) Anadyr River middle reaches; 14) Velikaya
 1935 River lower reaches; 15) Khatyrka River; 16) Pekul'neiskoe Lake; 17)
 1936 south Bering Peninsula; 18) Ugol'naya Bay; 19) Amaam Lagoon; 20)
 1937 Corwin Bluffs area; 21) Utukok, Kokolik, Kukpowruk Rivers; 22) Kuk -
 1938 Kaolak area; 23) Yukon-Koyukuk Basin; 24) Denali; 25) Colville (Umiat)
 1939 - Chandler River region; 26) Sagavanirktok River area.

1940

1941 Figure 3. Chronostratigraphic column for the late Albian and Late Cretaceous
 1942 of the Colville Basin, North Slope, Alaska, based on Mull et al. (2003).

1943

1944 Figure 4. Correlation chart for Albian to Paleocene deposits of the Arctic
 1945 Slope of N. Alaska: (l) lower, (m) middle, (u) upper. LU – Lithological
 1946 Unit of Smiley (1966). Modified from Herman (2007b).

1947

1948 Figure 5. Correlation chart for Albian and some Cenomanian floras of
 1949 Northeastern Russia and Northern Alaska. Modified from Herman
 1950 (2007c).

1951

1952 Figure 6. Correlation chart for upper Albian to early Paleocene deposits in
 1953 N.E. Russia (the Anadyr-Koryak subregion): (l) lower, (m) middle, (u)
 1954 upper. Modified from Herman (2007a).

1955

1956 Figure 7. Correlation chart of N.E. Russia and N. Alaska regional floras.
 1957 Similar shades of grey indicate similar floral composition. Arrows
 1958 indicate floral connections/migrations. Modified from Herman (2007c).
 1959
 1960 Figure 8. The Arctic light regime with present day obliquity showing the
 1961 number of hours of daylight per 24 hour period throughout the year
 1962 (Anonymous, 1978).
 1963
 1964 Figure 9. Graph showing the MAT palaeolatitudinal temperature gradients for
 1965 floras grouped into age bins 98.6 – 95 Ma (Cenomanian), 90-85 Ma
 1966 (Turonian – Coniacian) and 70 Ma (Maastrichtian). Internally consistent
 1967 palaeolatitudes for these age intervals were obtained using
 1968 PointTracker v.5.5 supplied by C. Scotese. The ages and
 1969 palaeolatitudes used here are shown after the name of the flora.
 1970 Teretky-Sai (Kazakhstan) (95 Ma: 42 °N); Vilui Basin (Siberia) (95 Ma:
 1971 68 °N); Tuscaloosa (Alabama) (95 Ma: 32 °N); Woodbine (Texas) (95
 1972 Ma: 32 °N); Chucle and Vyshehoroviche (Czech Republic) (95 Ma:
 1973 40°N); Grebenka (98.6 Ma: 81°N); Kaysayam (Kamchataka) (88 Ma: 72
 1974 °N); Penslina (Kamchataka) (90 Ma; 72 °N); Tuluvak (N. Slope) (88 Ma:
 1975 80 °N); Arman River (N.E. Russia) (88 Ma: 68 °N); Tylpergergenai
 1976 (N.E. Russia) (88 Ma: 79 °N); CzechSen (85 Ma: 39 °N); Lance
 1977 (Wyoming) (70 Ma: 49 °N); Ripley (Mississippi) (70 Ma: 38 °N); Denali
 1978 (Alaska) (70 Ma: 74 °N) (data from Tomsich et al. this volume); Cooper
 1979 Pit (Alabama) (70 Ma: 36 °N); Edmonton (Canada) (70 Ma: 55 °N)
 1980 (data from Tomsich et al. this volume). Regression equations -

1981 Cenomanian $y = -0.1421x + 23.348$, R^2 0.909, 2σ of residuals 1.08 °C;
 1982 Turonian-Coniacian $y = -0.1674x + 22.434$, R^2 0.809, 2σ of residuals
 1983 2.6°C. Maastrichtian $y = -0.1947x + 22.242$, R^2 0.9716, 2σ of residuals
 1984 0.36 °C.

1985 Figure 10. Graph showing the MAT /Age relationship derived from floras in
 1986 N.E. Russia and N. Alaska using floral composition, Leaf Margin
 1987 Analysis and CLAMP. The Arctic Ocean surface temperature estimate
 1988 (assumed to be MAT but possibly biased towards the WMMT) derived
 1989 from the TEX₈₆ proxy is also shown (Jenkyns et al., 2004).

1990

1991 Figure 11. Reconstruction of a summer scene at 70 Ma close to the Arctic
 1992 Ocean shoreline (80 – 85 °N).

1993

1994 Table 1. Palaeoclimate determinations for Late Cretaceous fossil floras using
 1995 CLAMP calibrated with global gridded climate data derived from New et
 1996 al. (1999) using the methodology of Spicer et al. (2009). The floras are
 1997 numbered as in Fig. 1. Abbreviations: MAT, warm month mean
 1998 temperature - WMMT, cold month mean temperature - CMMT, length
 1999 of the growing season - LGS, mean growing season precipitation -
 2000 GSP, mean monthly growing season precipitation - MMGSP,
 2001 precipitation during the three wettest months - 3-WET, precipitation
 2002 during the three driest months - 3-DRY, specific humidity - SH, relative
 2003 humidity - RH, enthalpy – ENTHAL and Palaeolatitude - P Lat.
 2004 Palaeolatitudes were obtained using Point Tracker supplied by C.
 2005 Scotese.

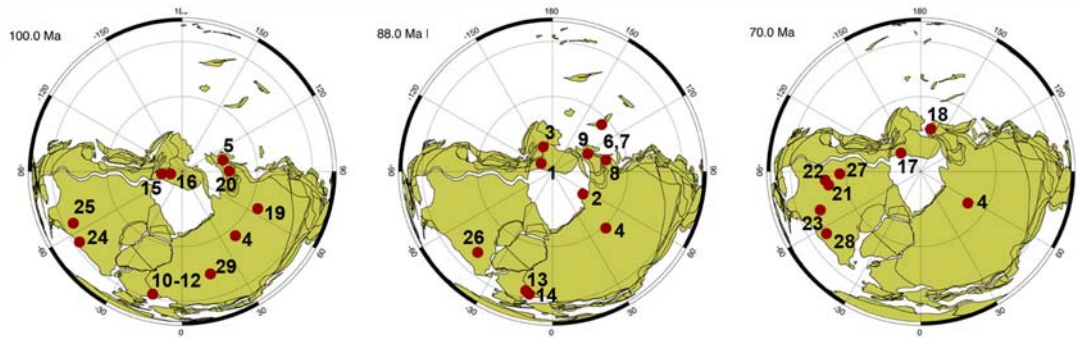


Figure 1

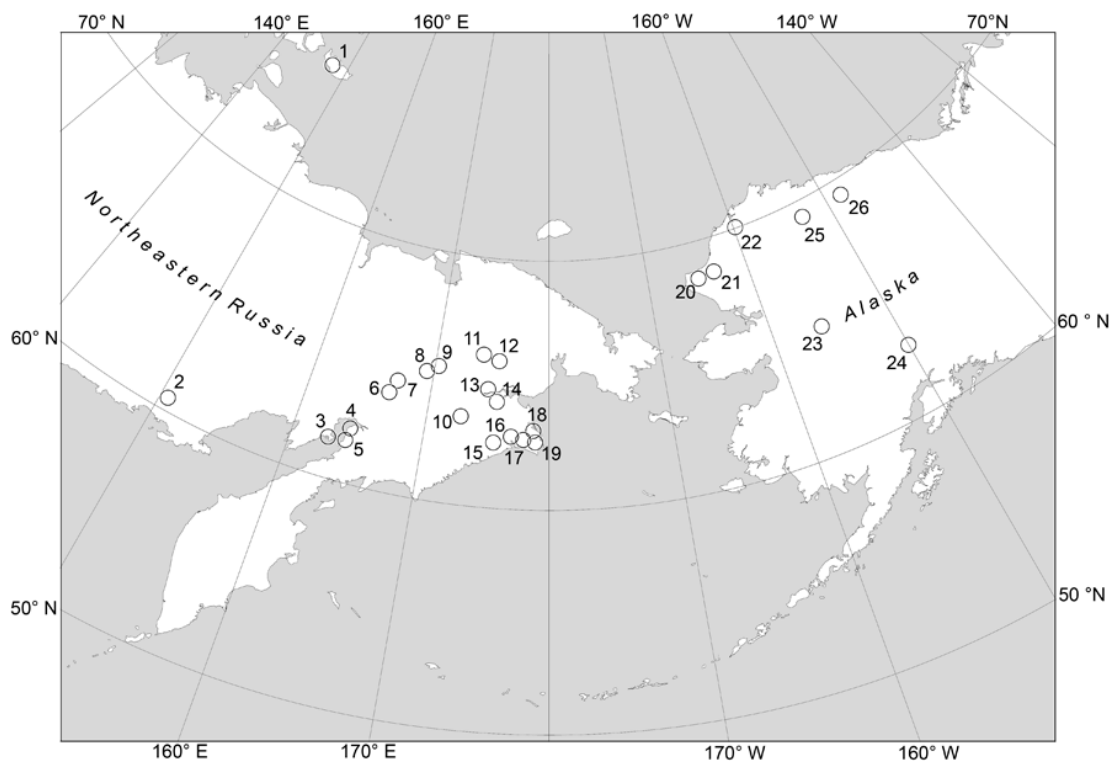


Figure 2

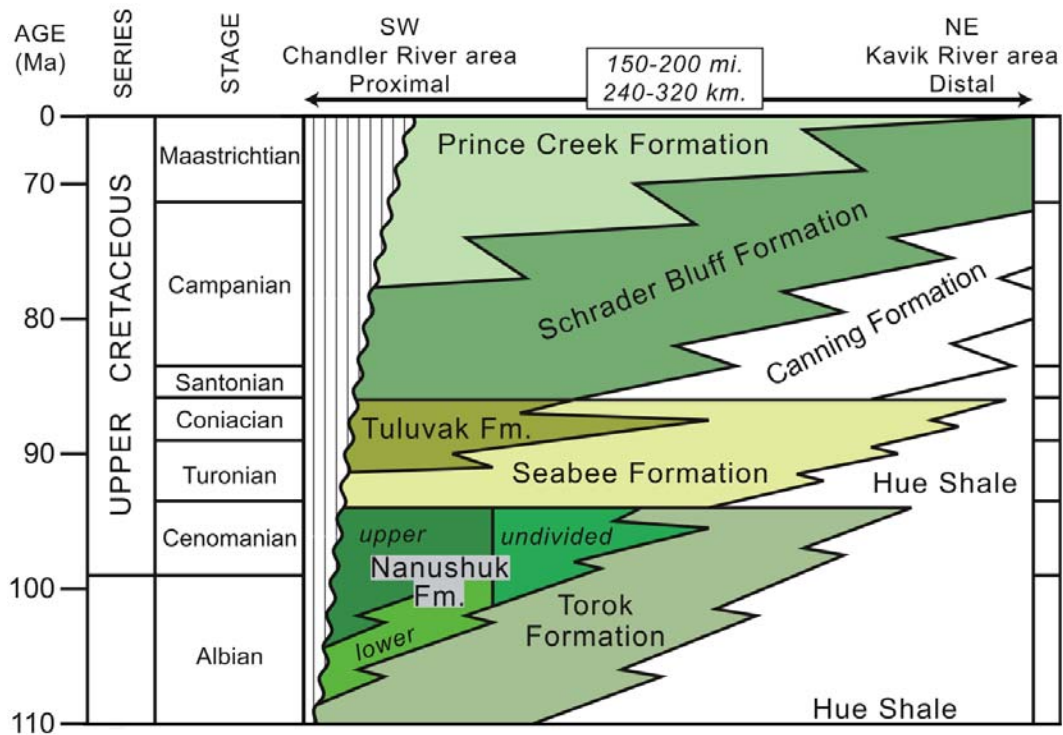


Figure 3.

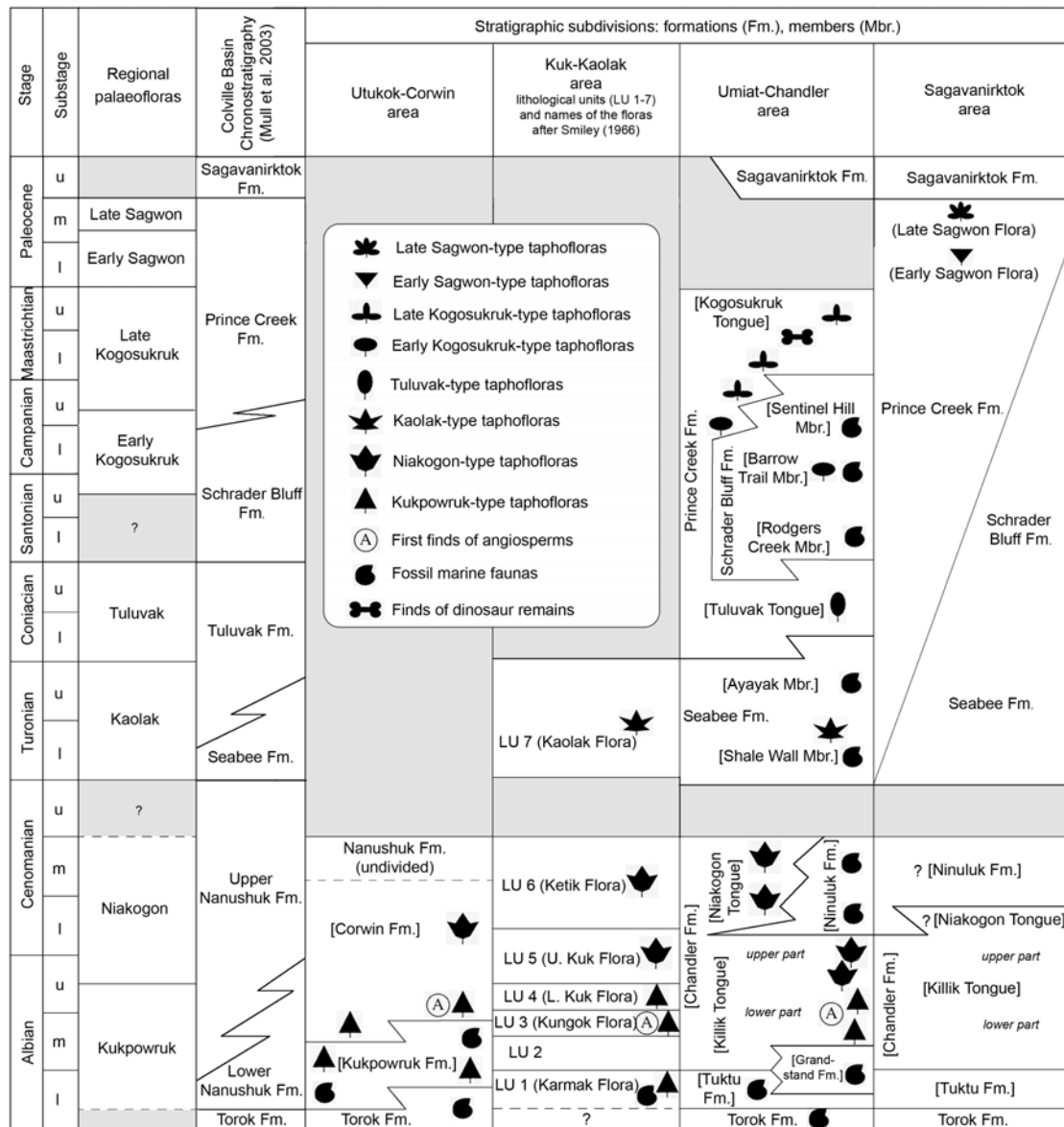


Figure 4.

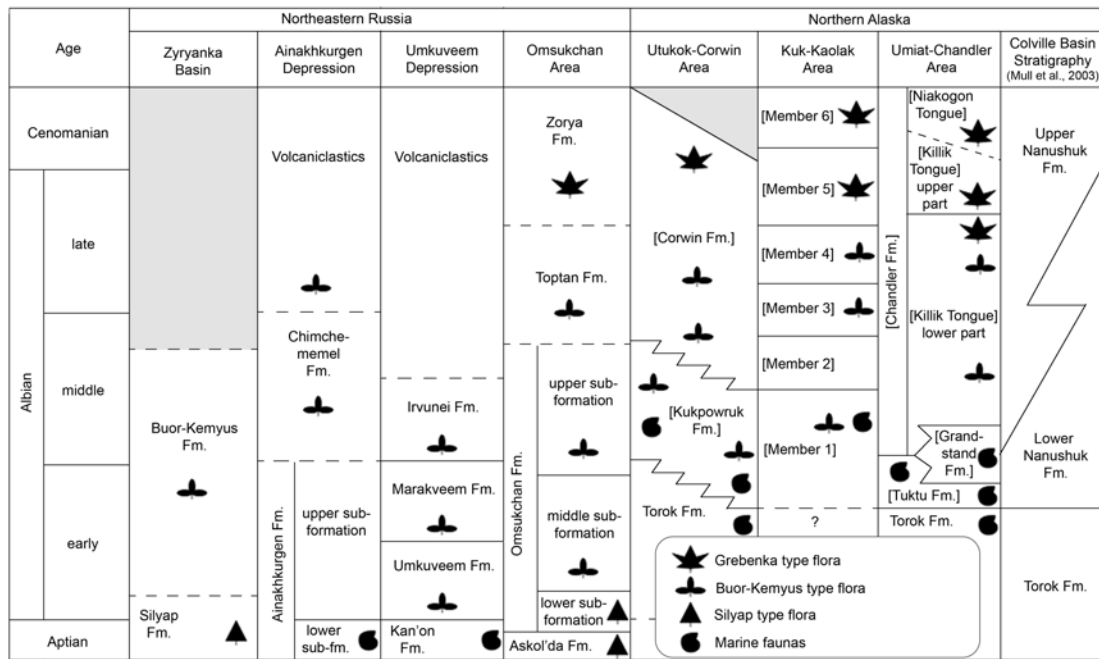


Figure 5.

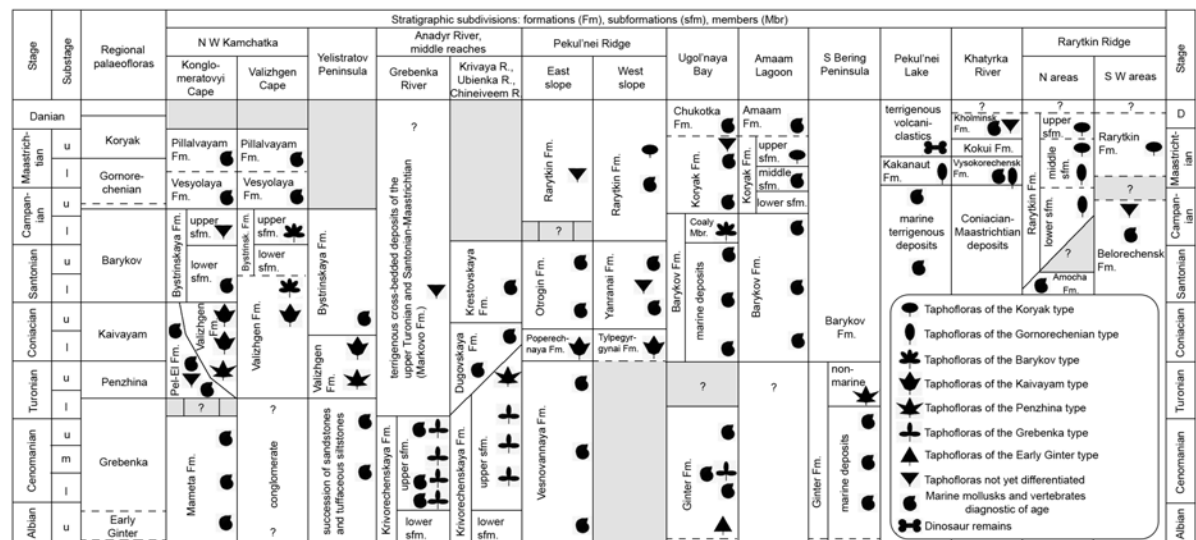


Figure 6.

Stage	Substage	Regional palaeofloras										Stage	
		Anadyr-Koryak region					Northern Alaska region						
Thanetian												Late Sagwon	Thanetian
Selandian												Early Sagwon	Selandian
Danian													Danian
Maastrichtian	upper	Koryak											Maastrichtian
	lower	Gornorechenian											
Campanian	upper	Barykov											Campanian
	lower												
Santonian	upper												Santonian
	lower												
Coniacian	upper	Kaivayam											Coniacian
	middle												
	lower												
Turonian	upper	Penzhina											Turonian
	middle												
	lower												
Cenomanian	upper	Grebenka											Cenomanian
	middle												
	lower												
Albian	upper	Early Ginter											Albian
	middle												
	lower												

2023

2024 Figure 7.

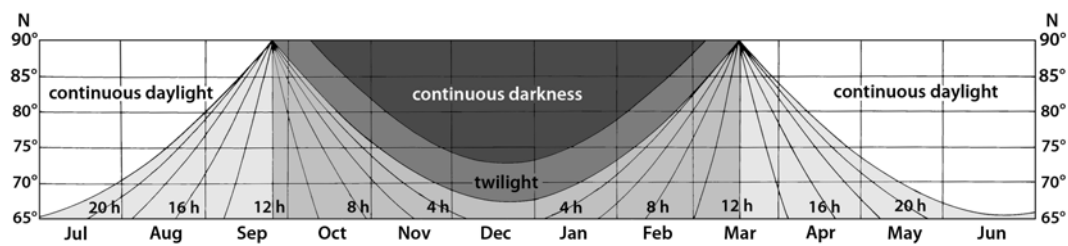


Figure 8.

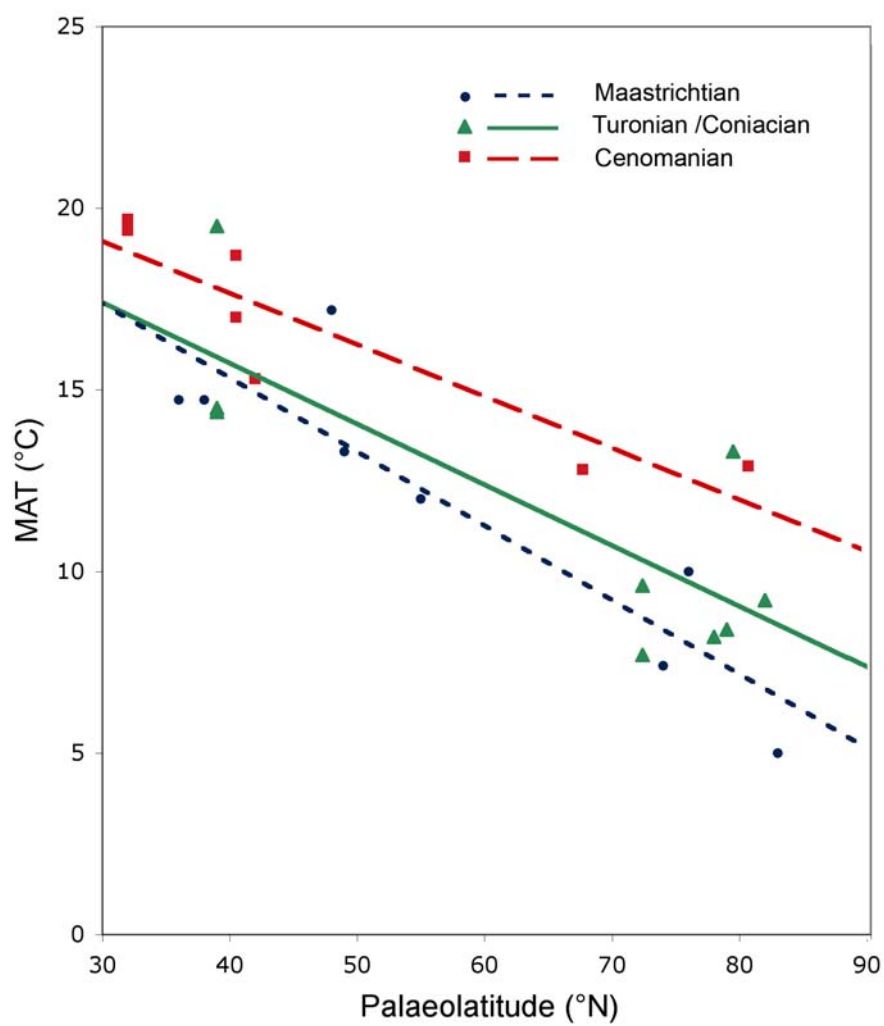


Figure 9.

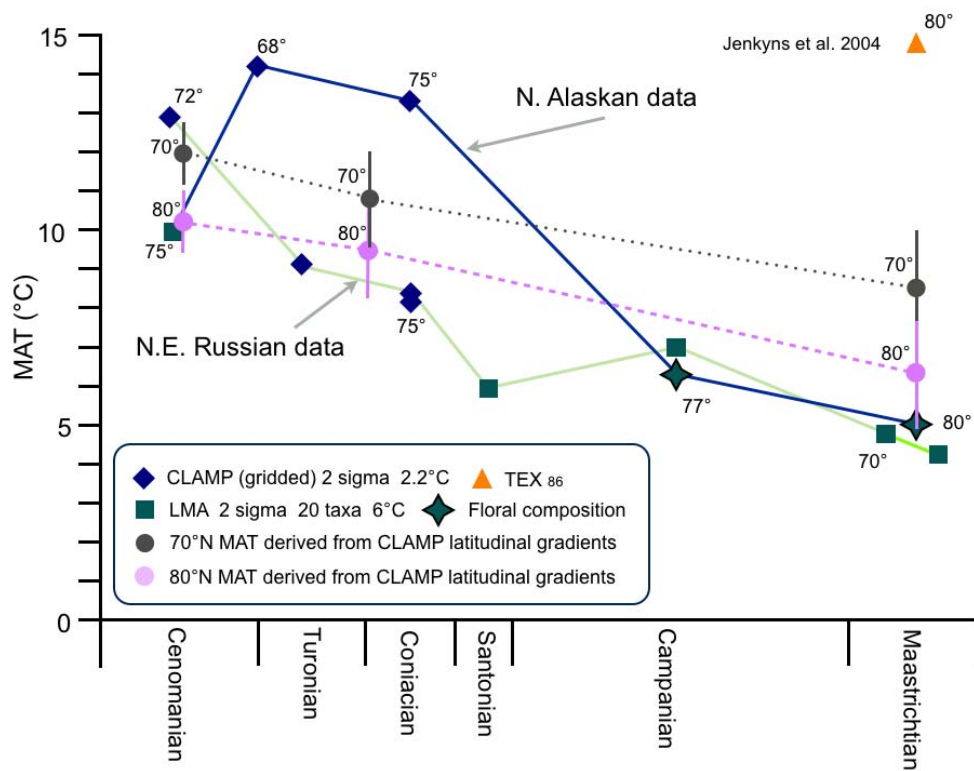


Figure 10.



Figure 10.

FLORA (Age Ma)	MAT (°C)	WMMT (°C)	CMMT (°C)	LGS (months)	GSP (mm)	MMGSP (mm)	3WET (mm)	3DRY (mm)	RH (%)	SH (g/kg)	ENTHAL (kJ/kg)	P.Lat (°N)
1. N. Alaska (88	13.3	19.1	7.9	7.6	793	88	526	184	80.4	10.1	326	80
2. Nov. Sibir (90)	9.2	17.2	1.1	5.8	537	79	504	151	76.7	7.0	310	82
3. Yukon (90)	14.3	21.1	8.0	8.1	1248	158	619	267	84.9	12.4	336	73
4. Vilui B. (95)	12.8	21.0	5.3	7.4	1054	135	623	209	79.9	9.6	324	68
5. Grebenka (98)	12.9	20.8	5.9	7.4	823	93	577	145	72.5	8.0	317	81
6. Kamchatka (90)	7.7	17.7	-2.4	5.1	427	82	466	144	75.4	5.8	304	72
7. Kamchatka (88)	9.6	18.3	1.1	6.0	598	88	519	154	76.0	7.0	310	72
8. Arman R. (88)	8.2	18.7	-2.0	5.3	481	88	481	143	74.1	5.8	304	68
9. Tylpegyrgynai (88)	8.4	18.8	-1.6	5.4	476	82	493	126	71.2	5.3	303	79
10. Chuchle (95)	18.7	27.3	10.4	10.1	1432	158	676	170	67.6	9.4	329	41
11. Vyshehor. (95)	17.0	26.2	8.3	9.4	1786	210	825	231	75.6	10.4	331	41
12. Peruc (95)	16.2	26.2	7.2	8.9	1208	146	631	162	67.9	8.4	322	41
13. Grunbach (80)	14.4	26.7	3.2	8.1	1196	165	654	154	63.6	6.8	314	39
14. Czechsen (85)	14.5	28.7	0.9	8.2	1357	199	707	146	54.9	5.4	309	39
21. Lance (70)	13.3	22.2	5.3	7.6	793	100	540	144	71.6	7.7	317	49
22. Medicine B. (70)	17.2	23.6	11.2	9.4	1440	152	713	218	79.0	11.0	333	48
23. Ripley (70)	14.7	25.3	5.3	8.3	983	119	623	109	57.6	6.3	312	38
24. Tuscaloosa (95)	19.7	24.5	15.1	10.5	1456	131	696	195	76	11.6	338	32
25. Woodbine (95)	19.4	23.5	15.4	10.3	1305	104	686	160	72.3	10.8	334	32
26. Gayhead (84)	19.5	24.3	14.8	10.4	1551	133	794	171	70.4	10.6	334	39
28. Cooper (70)	14.7	25.3	5.3	8.3	983	119	623	108	57.6	6.3	312	36
29. Terekty-Sai (95)	15.3	22.2	9.2	8.5	1070	120	600	191	78	10.3	310	42

STDEV Residuals	1.1	1.4	1.9	0.7	196	26	138	32	5.2	1.0	5	≈ 5
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